Context Dependence in the Habitat Relationships of Coastal and Marine Fishes

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“Biology is fast approaching maturity. It is time that we biologists accept diversity and variability for what they are, two of the essential features of the biological world. We would be wise to restructure our search for orderly patterns in the natural world. We should stop thinking primarily in terms of central tendencies. Instead of viewing the variance in our data with despair, we should regard it with satisfaction… Analysis of this variation can offer insights just as surely as can traditional delineation of central tendencies… [Biologists] have little choice but to rejoice in variability and diversity, for they are integral parts of the system they study.”

– George A. Bartholomew, 1986

Statement of the contribution of others

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Abstract

Coastal habitats support fish and invertebrate populations globally. However, the kinds of habitats that fauna use, and how they use them, can differ between locations. Fauna-habitat relationships are not homogeneous. Given their heterogeneity, there are limits on the generality and transferability of habitat relationships. This variability presents a serious obstacle for understanding the role that habitats play in supporting fauna, and the requirements that fauna have for habitat.

In this thesis, I explore whether fauna-habitat relationships may be predictable based on environmental context. I develop, test and apply the concept of *context-dependence* to fish communities in coastal habitats throughout the Indo-Pacific, using mangroves as a case study in my final chapters. I develop a novel heuristic approach for understanding context-dependence in habitat use by fauna, that can provide a quantitative, measurable yardstick to establish the relevance of particular relationships.

A cohesive understanding of variability in fish habitat use has been hindered by a lack of comparable data from different environments and regions. I employed a uniform technique, remote underwater video census, throughout the range of environmental variability found in coastal seascapes in the Indo-Pacific. This allowed me to directly compare fish presence and abundance across a range of different habitats and contexts for the first time, collecting more than 2,000 video samples across five regions. Overall, my results revealed that context-dependence in habitat relationships is a widespread feature of fish-habitat relationships in tropical nearshore ecosystems.

Within a single region, the Hinchinbrook and Palm islands of the Great Barrier Reef coast, a range of similar structural habitat types are present in both estuarine and marine contexts. Across this region, I found that context was more important in determining juvenile fish assemblages than the kind of habitat forming substratum or biota that were present. Similar habitat types in different contexts were functionally distinct; marine and estuarine mangroves contained entirely different assemblages of juvenile fish, and likewise for rocky reefs and submerged aquatic vegetation.

Throughout the Indo-Pacific, context-dependence explained a large proportion of variability in the relationships between fish and mangroves. Across a range of locations within northern Australia, Papua New Guinea and Polynesia, I found substantial variation in family level taxonomic associations with mangrove habitat. The magnitude of variation in the composition of fish assemblages was similar both within and across regions, and much of this variation was related to differences in salinity, seascape structure and tidal regimes. I observed consistencies in mangrove utilisation in similar environmental contexts despite geographic separation. For example, there were strong commonalities in the taxonomic composition of assemblages found in areas close to reefs that experienced small tidal ranges, and also strong commonalities in assemblages found in areas far from reefs that experienced large tidal ranges.

Across these same regions within the Indo-Pacific, I found clear and unique environmental thresholds in the use of mangroves by different fish functional groups. Using the heuristic framework developed in this thesis, I defined context-dependence in the use of a common mangrove habitat feature, fringing *Rhizophora* prop roots. The use of this habitat by reef fish was dependent on both its distance from reef habitat, and tidal amplitude. In contrast, the use of this habitat by coastal and estuarine fish was instead dependent on salinity. The ecological functional diversity of fish assemblages in fringing *Rhizophora* habitat was also dependent on these contextual factors. There was a diversity of feeding groups and body sizes in areas close to reefs that experienced small tidal amplitudes, whereas zoobenthivores and large body sizes dominated locations that were far from reefs or experienced large tidal amplitudes. Together, this suggests that the ecological roles played by certain habitat or vegetation types can be dependent on environmental context.

Overall, context-dependence in fish-habitat relationships implies that patches of the same habitat type may not fill the same ecological role for fish in different locations. The interlinked set of paradigms and management practices that relate nearshore habitat to ecological outcomes such as productivity and fisheries yield, need to be evaluated in light of this variability. Context-dependence also implies that certain environmental drivers can broadly define nearshore ecosystem function. My research highlights that notions of the role that habitat features play in supporting fauna, and the requirements that fauna have for habitat, may be transferable between equivalent environmental contexts, despite geographic separation.

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Outputs generated during my candidature

Publications arising from chapters in this thesis

Chapter 2:

Bradley, Michael, Ivan Nagelkerken, Ron Baker and Marcus Sheaves. (under review) "Context-dependence: a conceptual approach for understanding the habitat relationships of coastal marine fauna." *Fish and Fisheries*

Chapter 4:

Bradley, Michael, Ron Baker, Ivan Nagelkerken and Marcus Sheaves. (2019) "Context is more important than habitat type in determining use by juvenile fish." *Landscape Ecology* 34: 427-442

Chapter 5:

Bradley, Michael, Ivan Nagelkerken, Ron Baker and Marcus Sheaves. (in prep) “Local context explains variability in mangrove fish assemblages across multiple scales throughout the Indo-Pacific.”

Chapter 6:

Bradley, Michael, Marcus Sheaves, Ron Baker and Ivan Nagelkerken. (in prep) “Habitat context predicts the use of mangroves by fishes.”

Publications incorporating data from this thesis

Baker, Ronald, Adam Barnett, **Michael Bradley**, Katya Abrantes, and Marcus Sheaves. (2019) "Contrasting Seascape Use by a Coastal Fish Assemblage: a Multi-methods Approach." *Estuaries and Coasts* 42: 292-307.

Christopher J. Fulton, Charlotte Berkström, Shaun K. Wilson, Rene Abesamis, Carolina Akerlund, Luke Barrett, **Michael Bradley**, Abner Bucol, Dinorah Chacin, Karen Chong-Seng, Darren Coker, Martialla Depczynski, Linda Eggertsen, Maria Eggertsen, David Ellis, Richard Evans, Nicholas Graham, Andrew S. Hoey, Thomas H. Holmes, Michel Kulbicki, Priscilla T. Y. Leung, Paul K. S. Lam, Joshua van Lier, Paloma Matis, Mae M. Noble, Alejandro Perez-Matus, Camilla Piggott, Benjamima T. Radford, Michael Rule, Stina Tano, Paulina Tinkler. (in prep) "Macroalgal habitats facilitate tropical fish diversity and productivity"

Reports arising from this thesis

During candidature, findings from data collected in this thesis were reported to governmental authorities to inform fisheries management.

Fisheries Research and Development Corporation, Australia (FRDC):

Sheaves, Marcus, Adam Barnett A, **Michael Bradley**, Katya Abrantes, Martha Brians. (2016) Final Report – project number 2013-046 - Life history specific habitat utilisation of tropical fisheries species.

Bradley, Michael, Marcus Sheaves (2016) Final Report – project number 2013-046 - Critical Fisheries Habitat: Developing Detailed Models of Life-History Habitat Utilization Via Large-Scale Video Analysis

Australian Centre for International Agricultural Research (ACIAR):

Sheaves, Marcus, Adam Barnett, Katya Abrantes, Jacob Wani, Amy Diedrich, Ron Baker, Carlo Mattone, **Michael Bradley**, Lina Pandihau. (2018) Final Report for the FIS/2013/015- "Sustainable Management of Sportfisheries for Communities in Papua New Guinea"

Other outputs during candidature

Michael Bradley, Ingrid van Putten, Marcus Sheaves. (2015) "The pace and progress of adaptation: Marine climate change preparedness in Australia's coastal communities" *Marine Policy* 53: 13-20

Michael Bradley, Ron Baker, Marcus Sheaves. (2017) "Hidden components in tropical seascapes: deep-estuary habitats support unique fish assemblages" *Estuaries and Coasts* 40: 1195-1206

Ronald Baker, **Michael Bradley**, Stefano Freddi, Katya Abrantes, Adam Barnett, Marcus Sheaves. (2018) "Non-lethal aging of tropical catch-and-release sport fishery species" *Fisheries Research* 207: 110-117

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1 General Introduction

1.1 Fauna-habitat relationships

Animals are inextricably linked to their habitats. Terrestrial and aquatic animals rely on their preferred habitat types for food and refuge, and many other functions. For example, mangroves provide nursery grounds for coral reef fish (Nagelkerken et al. 2000c), while particular areas of the ocean with deep, strong thermoclines function as feeding grounds for piscivorous seabirds (Vilchis et al. 2006). Relationships of fauna to habitat can be highly specialised. For instance, some species of birdwing butterflies rely on specific vine species during larval development, so their continued persistence in an area hinges directly on the presence of these plants (Sands and New 2013). If a particular habitat type is removed, it can lead to the extinction of species and re-structure communities (Coleman and Williams 2002). As a consequence, habitat destruction is already the main cause of faunal extinction on land (Ehrlich et al. 1983, Pimm and Raven 2000), and will soon be the biggest threat to ocean fauna (McCauley et al. 2015).

Models of fauna-habitat relationships are in essence reductionist models that seek to describe small parts of large and complex systems. Important associations between animals and habitat features (e.g. landforms, forest types, particular biogenic structures) are understood as expression of the ecological niche of a species within an ecosystem (Odum 1959). As a reflection of the functional interactions between an animal and the environment, animal-habitat relationships describe the parts of the environment required for population persistence within a location (Morrison et al. 2012). Models of these relationships are essential tools for predicting and managing natural systems. By modelling these relationships, ecologists define the features of the environment that are important to fauna and, concomitantly, the role that these features play as habitat for fauna in the ecosystem. These relationships form the basis for predicting both species and community response to change (Olden and Jackson 2001, Villéger et al. 2010), understanding ecosystem functioning (Dobson et al. 2006), and landscape resilience (Cumming 2011), all of which inform the management of these systems for both conservation and sustainable exploitation. Accordingly, protecting the specific habitats that fish require throughout their life-cycle has become a cornerstone in the management of coastal fish and fisheries (Rosenberg et al. 2000, Pikitch et al. 2004).

1.2 Variability in fauna-habitat relationships

Fauna-habitat relationships are not straightforward, because they vary from place to place. The habitat types involved in a relationship (McAlpine et al. 2008), the ways habitats are used (Rozas 1995, Kneib 2003), and the amount of habitat required for presence or persistence of a species (Rhodes et al. 2008) all differ between regions and ecosystems. For example, along the east coast of North America the relative importance of different habitat

types for fisheries species shifts between regions (Kritzer et al. 2016). Individual species may employ different habitat utilisation strategies in different locations. For example, both amphibian and reptile species can shift from ground-dwelling to arboreal at different altitudes (Adolph 1990, Scheffers et al. 2013). Therefore, in different locations, a species' dependence on a particular habitat type could be obligate, facultative, or even non-existent.

Heterogeneity in any sort of ecological relationship imposes limits on the generality and transferability of models of that relationship. It is possible to produce detailed and accurate models of fauna-habitat relationships, yet these will often be locally specific due to geographic variability (Fielding and Haworth 1995, Randin et al. 2006). The transferability of these models to different locations is rarely tested, so, the generality of these kinds of models tend to remain unknown (Wenger and Olden 2012). Because of this, many ecologists are reluctant to generalise findings about pattern or process in habitat function at all (e.g. Whittingham et al. 2003). On the other hand, this problem is often ignored, and untested potentially locally specific models can become the building blocks of broad paradigms about fauna-habitat relationships, which are often developed by combining findings from a range of different locations (Sheaves 2012). Both ways of dealing with, or rather failing to deal with, variability in habitat relationships impede progress in ecology. Without a detailed understanding of the limits on the generality and transferability of models, it is not possible to know where and when models of habitat relationships are valid, and how they can be incorporated into general understandings of ecosystem function. Variability in fauna-habitat relationships has called into question key paradigms around the role of different habitat types in coastal and nearshore ecosystems. In particular, the role that mangroves and seagrass play in supporting fish populations appears to vary considerably from place to place, with serious

implications for how the integrity of fisheries are managed (Saenger et al. 2013, Sheaves 2017). Improving the generality and transferability of models is a key concern in the study of fauna-habitat relationships throughout ecology (Thomas and Bovee 1993, Vaughan and Ormerod 2005), and is the driving focus of the research presented in this thesis.

1.3 Understanding variability in fauna-habitat relationships

Defining the limits of our understanding of fauna-habitat relationships is an important task in ecology. In the most basic sense, both the animal and habitat feature must first be present in an area for an association to exist. For an animal to be present in a location, three things are necessary; 1) connectivity (i.e. the animal must be able to access the location), 2) appropriate physical conditions (i.e. the animal must be able to survive in the location) and 3) appropriate resources (i.e. the animal must be able to access what it needs to persist). There are several major sources of geographic variation in fauna-habitat relationships. The large-scale distribution of a species is the product of historical biogeographic forces. The response of populations to the environment over geological time scales has produced the distribution of animals that we observe today, and current environmental and geographic limits to dispersal maintain these distributions (Morrison et al. 2012). These forces can explain why a species might be associated with a particular habitat type in some locations and not others. Therefore, any understanding of the use of habitat may be limited to the areas where similar species are present. The response to this limitation is to define bioregions where ecosystems can be considered taxonomically 'equivalent' (e.g. Sheaves 2012), and build understanding within, but not across these regional boundaries. In places where both the animal and habitat feature coincide, variation in use between locations can be due to variation in habitat quality. While

habitat might be of the same 'type' between locations, measurable differences in indices of habitat architecture and endogenous resources can result in differences in use (Moore et al. 2010, Nagelkerken et al. 2010). The response to this limitation is to further refine our understanding of what constitutes appropriate habitat (Johnson 2007). However, variation can also be due to factors that are external to the habitat. The context within which a patch of habitat occurs can lead to variation in fauna-habitat relationships, by changing the way that fauna interact with their environment. For example, whether in a river or on a reef, hydrodynamic energy can determine whether fish use sheltered habitat or exploit the open water column (Fulton and Bellwood 2005, Thorp et al. 2006, Johansen et al. 2008). The concept of context dependent habitat use is explored fully in Chapter 2. Dealing with this source of variation remains a challenge in nearshore ecosystems. While many different contextual sources of variation have been identified for particular relationships, it remains difficult to define accurate boundaries for understandings of habitat use. This is because the interplay of different contextual factors in determining habitat use at any particular location is poorly understood. To address this gap, the general aim of this thesis is to better understand the contextual component of variability in fish-habitat relationships in tropical nearshore ecosystems.

To achieve this broad aim, I will address the following specific objectives:

1) To develop a conceptual approach for examining contextual variability in the habitat relationships of coastal marine fauna

I address this objective by; a) synthesising diverse ecological theory to apply the concept of context-dependence to fauna-habitat relationships, b) reviewing literature on environmental variability in fish-habitat relationships to determine important contextual factors for fish, and c) developing a heuristic framework with which to define thresholds in fish-habitat relationships (Chapter 2). I then apply and evaluate this new conceptual approach throughout the thesis in my data-based research chapters.

Before I introduce my data-based research chapters, I detail the specific data requirements of this thesis, and the methodology used to fulfil those requirements (Chapter 3).

2) Define the extent of variability in habitat relationships in nearshore environments, and test whether this variation relates to specific aspects of environmental context.

I first address this objective by exploring variation in fish-habitat relationships across the heterogeneous landscapes found throughout a region. Here I test whether contextual factors structure faunal relationships for a range of different nearshore habitat types (Chapter 4). I then address this objective by exploring variation in fish-habitat use of a single habitat type (mangroves) throughout the Indo-Pacific. Here I test whether contextual factors can explain variation in fish habitat use across biogeographic scales (Chapter 5).

3) Define contextual boundaries in the use of habitat by particular fauna.

I address this objective by using the heuristic approach developed in Chapter 2. Here I define contextual thresholds for the use of mangroves by different fish functional groups, and use

this to make concrete predictions about the ecological role of mangroves in different coastal environments (Chapter 6).

Overall, fish-habitat relationships appear to be highly dependent on environmental context, and this has important implications for our understanding of tropical nearshore ecosystems, how they function, and how to maintain their remarkable value in the face of anthropogenic disturbance.

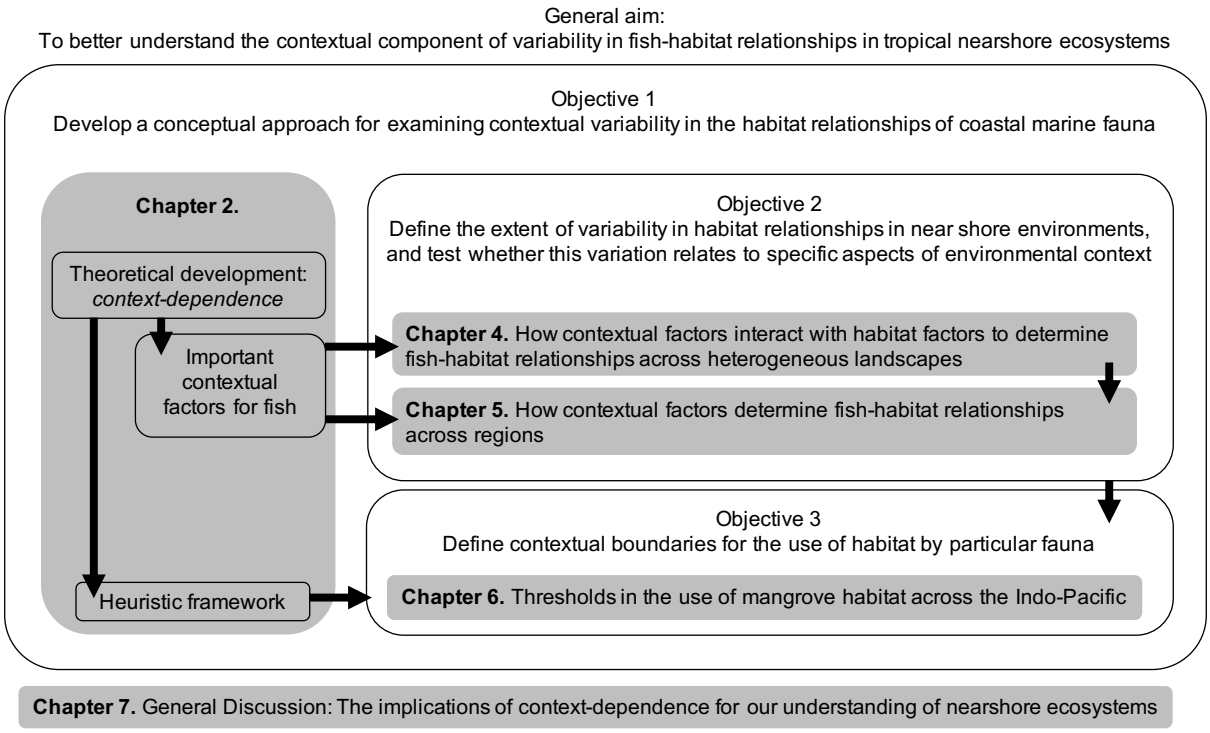
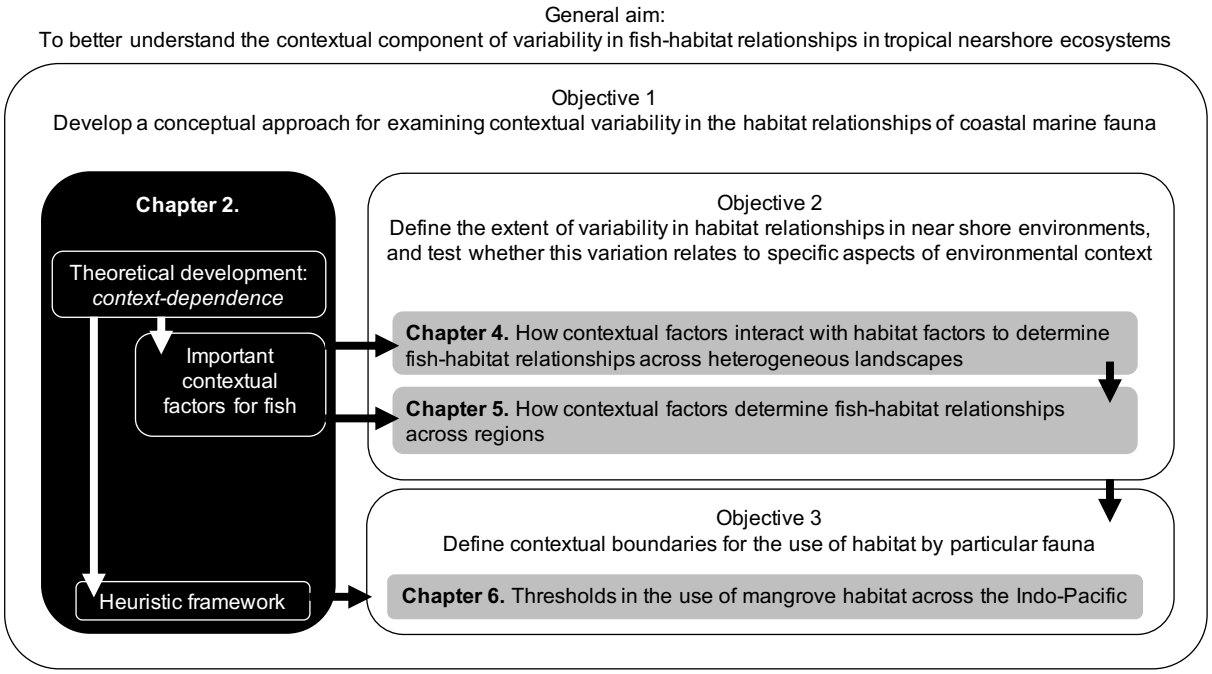


Figure 1.1 Thesis structure.

Conceptual diagram shows my thesis objectives and the chapters that address them. Arrows depict how concepts or information developed in one section of the thesis informs subsequent sections. This diagram is repeated at the beginning of each chapter, with the relevant chapter highlighted.

2 Context-dependence: a conceptual approach for understanding the habitat relationships of coastal marine fauna



Abstract

Coastal freshwater, estuarine and marine habitats underpin fish and invertebrate populations globally. Understanding the role that habitats play in supporting fauna, and the requirements that certain fauna have for habitat, are key pursuits in ecology and key tools for conservation and fisheries management. But habitat relationships are not homogeneous, and can exhibit variability in space and time. Due to the complexity of ecological systems, context-dependence is a pervasive feature of ecological relationships. Employed as a conceptual tool in other areas of ecology, context-dependence is rarely examined in habitat relationships, where it is likely to be an important source of variability and a key ecological driver of animal communities. For fish in coastal marine and freshwater ecosystems, differences in context can indeed change both the reason habitat is used, and what goods and services a habitat can provide. This complicates the ways we can use and interpret fish-habitat relationships scientifically, and as the basis for management tools such as habitat protection, restoration and offsetting. However, it also implies that this complexity is reducible. Here, I propose a novel heuristic approach to developing a robust understanding of the context-dependence of habitat values. This can provide a quantitative, measurable yardstick to establish the spatiotemporal relevance of fauna-habitat relationships, producing useful ecological understanding and actionable knowledge for management. I detail how large-scale drivers of context, like tidal regime, rainfall and geomorphology, can be used to develop frameworks to direct research and synthesise understanding of habitat relationships across large regional boundaries.

2.1 Introduction

Fauna-habitat relationships are critical building blocks in our understanding of natural systems. Academics and practitioners in various disciplines often use models of fauna-habitat relationships developed by ecologists (Manel et al. 2001). For instance, much multi-disciplinary 'ecosystem services' literature draws on knowledge of the ecological functions of different habitats (Carpenter et al. 2009) to properly account for their role in human society. However, scientists and practitioners often lack a concrete measure of when knowledge of fauna-habitat relationships can be appropriately generalised, because models of these relationships rarely explicitly account for variability in context. Without an appropriate yardstick to measure when it is safe to generalise or not, it is difficult, and perhaps even dangerous, to use these relationships outside the locations where they were developed. Defining the limits of knowledge – i.e. developing this yardstick – is as important as generating knowledge in the first place. Unbounded, our knowledge cannot be used reliably.

To provide this yardstick, I propose studying the context-dependence of fauna-habitat relationships. Many authors have called for a deeper awareness of environmental context in habitat relationships (e.g. Fielding and Bell 1997, Murphy and Lovett-Doust 2004, McAlpine et al. 2008, Sheaves 2012, Litvin et al. 2018) and while progress has been made in some areas (e.g. Fausch et al. 2002), the role of context remains a complex and multifaceted problem for ecologists, and therefore requires both extensive empirical research and substantial theoretical development. In this chapter, I evaluate the concept of context-dependence broadly and detail how it relates to fish-habitat relationships in coastal freshwater, estuarine and marine environments. I propose a simple heuristic for addressing context-dependence,

which transforms the way empirical studies are used in the production of knowledge of fish habitat.

2.2 Context-dependence in ecological relationships

Context-dependence is a universal problem in ecology because it complicates our ability to generalise about biological and biophysical interactions. These interactions occur within a complex system of other interactions between living and non-living components of the environment – an ecosystem. The particular qualities and composition of the ecosystem provide context for the biological interaction. However, the outcomes of these interactions may vary depending on differences between systems (Tylianakis et al. 2008). In these complex systems, causal pathways are, in an absolute and practical sense, not completely knowable (Wimsatt 1994, Harris and Heathwaite 2005). Systems may appear outwardly similar (e.g. they may contain the same set of components we are studying) but the way they work (i.e. their underlying causal structure (sensu McCann 2007), may be fundamentally different. A set of components may interact with each other in different ways. When looking across multiple systems, distinct and system-specific relationships between components can appear as instances of the same phenomena while actually being driven by unrelated forces, known as *aliasing* (MacNally 1995). Likewise, the sets of components that interact with each other may vary between systems. I define context as *the qualities of an ecosystem that influence a biological or biophysical interaction of interest*. This includes factors we are aware of, factors we do not consider, and factors we do not know about. Context includes, but is not limited to, the physical and chemical, biological, ecological and human social factors

that define each system, from solar irradiance to trophic networks, and human governance structures.

Context-dependence is a pervasive feature of ecological relationships in general and some fields of ecology have begun to harness the study of context dependency to better understand patterns in nature. For instance, the field of mutualism has studied context dependency for two decades (Thompson 1988, Bronstein 1994). This work has shown that many paired interactions may only be mutually beneficial in some environments or situations, such as where nutrients are limited, or if a specific predator is involved. This is true of all kinds of interactions; predation interactions vary in magnitude, while putative 'competitive' and 'mutualistic' interactions can range from having positive to negative outcomes for the species involved (Chamberlain et al. 2014). The functional role of species within systems can vary according to context, with consequences for trophic structures (Pace et al. 1999, Wellnitz 2014) and the effect a species has on ecosystem processes, such as top-down control or nutrient subsidy (Vaughn et al. 2007, Marino et al. 2018). More broadly, the relationship between biodiversity itself and ecosystem functioning can also be context dependent (Cardinale et al. 2000). For example, the relationship between tree species diversity and rates of ecosystem processes are strongest in forests where water is scarce, and weaken when water is abundant (Ratcliffe et al. 2017). These findings impel us, and others (Chamberlain et al. 2014, Rasher et al. 2017), to move away from debates about average patterns and universal paradigms, towards the study of context-dependence itself. Studying context-dependence will allow us to describe and predict natural variation in ways that rapidly advance our understanding of ecological relationships.

2.3 Context-dependence as an important source of variability in fauna-habitat relationships

The use of the term *habitat* to date, obscures context dependency in fauna-habitat relationships. Theoretical literature defines the term as any aspect of the environment that allows an animal to exist by fulfilling that animal's range of requirements (e.g. Kearney 2006). However, this definition is difficult to use. For example, do we have to measure soil nitrogen every time we want to talk about brown bear or koala habitat? Most ecologists use the word habitat to refer to the structural component of the environment (Hall et al. 1997). The components of interest are diverse but often visually obvious, such as a vegetation type, a certain index of structural complexity, or a sediment grade, and are also usually defined at a scale relevant to the size of the organism. For fish fauna, habitat has been defined as 'the structural component of the environment that attracts organisms and serves as a centre of biological activity' (Peters and Cross 1992, Williams and Bax 2001).

The way that fauna-habitat relationships are modelled and used by ecologists makes them particularly vulnerable to context-dependence. Ecologists often abstract habitat components from the context in which they have been studied. For instance, many studies select certain components of the environment, at particular scales, with which to define a habitat relationship for an animal – such as vegetation type, soil type or substratum composition – and leave out others – from flood periodicity to the strength of the earth's magnetic field. While this abstraction gives the apparent ability to generalize, we may lose critical information on the contextual elements of the environment that govern the relationship of interest to us. Animals use habitats as a response to specific conditions, so these contextual

elements can govern the fauna's requirements for habitat, such as their food and refuge requirements, as well as a habitat's tendency to provision goods, such as food, and services, such as refuge. In two different contexts, the habitats that an animal uses, and what it uses them for can be different. This leads to habitat relationships that are clearly context specific, and to the potential for apparently similar, aliased relationships driven by different requirements (Figure 2.1).

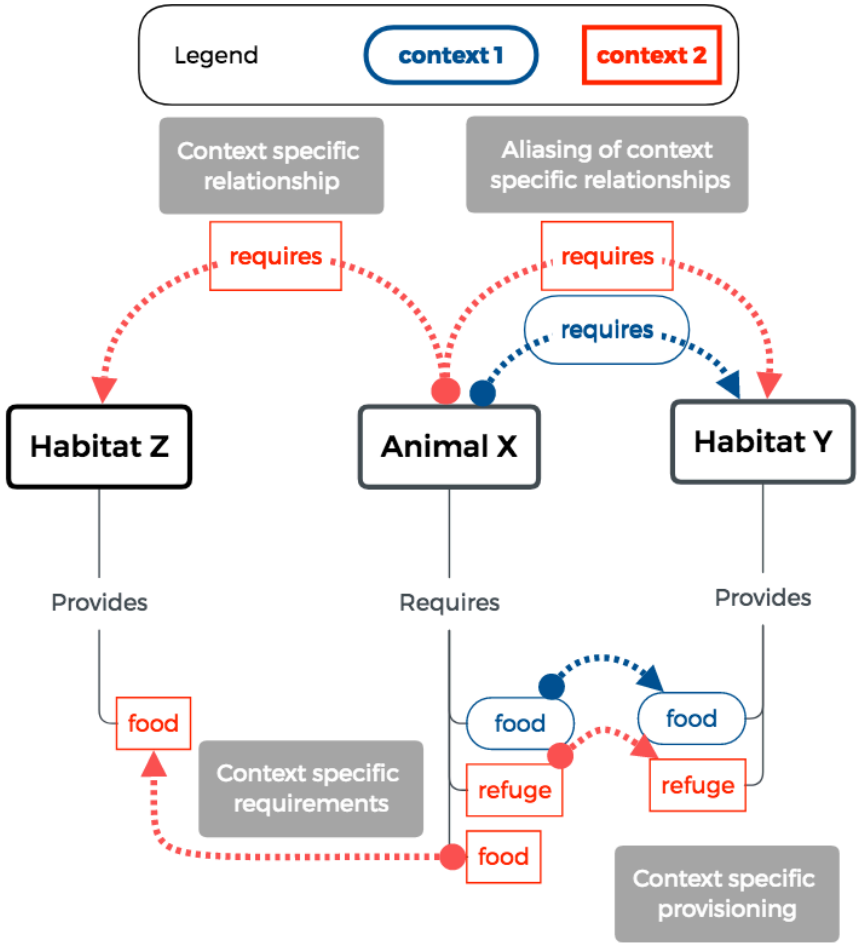


Figure 2.1. Simple conceptual scheme showing the context-dependence of a relationship between Animal X and Habitat Y.

Red arrows and text indicates the situation in one context, while blue arrows and text indicate the situation in another context. In both contexts, the animal uses Habitat Y, however, these responses are aliased as they are driven by different requirements. In context 2, the animal's requirement for food cannot be met by Habitat Y, so it requires a second habitat – Habitat Z.

2.4 Evidence of context-dependence in fish-habitat relationships

What evidence is there of context-dependence in fish-habitat relationships? For fish in coastal marine and freshwater ecosystems, differences in context can indeed change both why habitat is used, and what goods and services a habitat can provide. Following Chamberlain and colleagues (2014), different kinds of natural contextual variation can be captured with four broad categories:

1.Physical (e.g. nutrients, wave energy)

2.Ecological (e.g. species interactions such as the presence of predators)

3. Spatial (seascape configuration, e.g. isolation)

4. Temporal (periodicity, e.g. flooding)

2.4.1 Context and requirements

A fish's requirements for habitat can be shaped by its context. Fish use habitats as a response to specific conditions. For instance, physical factors can create stressors on fish that can be mediated by habitat use (Table 2.1, physical context). For example, intense sunlight necessitates the use of shade, provided by large table-corals on tropical reefs (Kerry and Bellwood 2015), and high wave energy necessitates the use of coral structure as a refuge (Bellwood and Wainwright 2001). Similarly, species interactions can drive habitat requirements (Table 2.1, ecological interaction context). For instance, the presence of a predator can determine the need for refuge. 'Landscapes of fear' lead to key differences in habitat use when predators are present or absent (Willems and Hill 2009, Laundré et al.

2010). For fish, predators tend to increase the use of structured habitats by prey (Gotceitas et al. 1995). The type of predators can also shape habitat use, with key differences in ambush and pursuit predators (Turner et al. 1999), and emergent effects of multiple predators (Sih et al. 1998).

The relative balance of factors that shape habitat requirements will shift across different contexts. For example, flow velocity is a major controlling variable of fish habitat use in freshwater systems (Bain et al. 1988, Chipps et al. 1994) where it directly influences whether habitat choice is based on flow refuge or predator avoidance (Shirvell 1990). This situation is mirrored on coral reefs (Bellwood et al. 2002), where a variety of fishes use structurally complex reef habitats in high wave energy environments (Johansen et al. 2008) in order to access food resources (Johansen et al. 2007). In low energy environments, these same fish do not need structured habitats and instead readily use the water column, but only in the absence of predators (Fulton et al. 2001, Krajewski et al. 2011). Therefore, in high flow or high energy contexts, habitat as hydrodynamic refuge becomes paramount, whereas in low energy contexts other facets of habitat function come to dominate habitat selection behaviour (e.g. the distribution of resources, predators and competitors). Similar effects have been observed for a range of other factors (Table 2.1, physical context) – all of which have the potential for producing aliased responses to habitat in fish.

The habitat requirements of an individual can shift through time. The physical and ecological contexts that shape habitat requirements as described above, can change over daily and seasonal timescales. Habitat requirements will also shift according to key biological and physiological changes that occur within the lifecycle of the fish. Ontogenetic changes in size

and morphology alter the resources that a fish can access within a habitat, leading to changing habitat requirements with ontogeny (Werner and Gilliam 1984). For example, body size determines the scale at which habitat architecture can provide refuge, while also limiting the size of prey that the fish can consume, and its energetic requirements. Key events such as spawning, demersal egg laying and brooding will all have their own temporally acute set of habitat requirements (Beard Jr and Carline 1991, Koenig et al. 2000, Gladstone 2007).

Table 2.1. The four main broad categories of ecosystem context for fish in coastal aquatic systems, with example factors, their potential impacts on habitat relationships, and example references.

Broad category:	example factor:	potential impact on habitat relationships:	example reference:
Physical	salinity	restricts habitat use	(Martino and Able 2003),
		drives movement between habitats	(Cyrus and Blaber 1992, Whitfield et al. 2006)
	temperature	restricts habitat use (extreme high or low)	(Attrill and Power 2004)
		drives habitat use (thermal optima)	(Sims et al. 2006)
	dissolved oxygen	restricts habitat use	(Eby and Crowder 2002)
		Low values necessitate movement between habitats	(Hasler et al. 2009).
	water depth	restricts habitat use	(Somero 1992, Bradley et al. 2017)
	solar irradiance	can necessitate the use of shade, positive relationship with shade providing habitat use	(Verweij et al. 2006, Kerry and Bellwood 2015)
	wave energy	can have a negative relationship with diversity of habitats used, positive relationship with structured habitat use	(Shirvell 1990, Fulton et al. 2001, Bellwood et al. 2002, Johansen et al. 2008)
	Soundscapes	biological soundscapes; effects habitat selection	(Huijbers et al. 2012)
		artificial soundscapes; negative relationship with habitat use	(Slabbekoorn et al. 2010)
	artificial light	positive relationship with habitat use	(Becker et al. 2013).
	water movement	positive relationship with structured habitat use	(Bain et al. 1988, Williams and Bax 2001, Ensign and Doyle 2006, Thorp et al. 2006)

		influences physical conditions	(Officer 1981, Jorgensen and Des Marais 1990, Decho 2000, Bouillon et al. 2007)
		influences the distribution of food resources in time and space	(Hamner et al. 1988, O'Brien and Showalter 1993, Noda et al. 1994, Ackerman et al. 2000, Mendes et al. 2002)
		negative relationship with diversity of habitats used, influences home-range size	(Minns 1995, Meyer et al. 2007, Woolnough et al. 2009)
	Dissolved nutrients	influences food resource availability	(Paerl et al. 1999)
Ecological (species-interactions)	predator environment	restricts habitat use, generally positive relationship with structured habitat use	(Shirvell 1990, Gotceitas et al. 1995, Turner et al. 1999)
	food availability	positive relationship with habitat use, interactive with other contextual factors	(Abrahams and Dill 1989)
	competitor environment	restricts habitat use, negative relationship with diversity of habitats used	(Hixon 1980, Hughes 1992, Nakano 1995, Webster and Hixon 2000, Hesthagen and Heggenes 2003, David et al. 2007)
	mutualisms and symbioses	absence of partner species can restrict habitat use	(Sun et al. 2015)
	availability of spawning/nesting habitat	restricts use of otherwise suitable adult habitat	(Beard Jr and Carline 1991)
	social environment	absence of conspecifics can restrict habitat use	(Bietz 1981)
Spatial	isolation	modifies predation effects, regulates use of habitat	(Overholtzer-McLeod 2006)
	patch size	modifies predation effects, regulates use of habitat	(Hovel and Regan 2008)
	configuration	regulates use of habitat	(Pittman et al. 2004)
	presence of a second habitat type	regulates use of habitat	(Dorenbosch et al. 2007, Luo et al. 2009)
Temporal	periodic variation in physical conditions (e.g. seasonality, disturbance events)	positive relationship with diversity of habitats used	(Copp 1992, Allouche 2002, Vilizzi et al. 2004)
	periodic variation in availability of habitat	positive relationship with diversity of habitats used	(Gibson 1992, Sheaves 2005)
		positive relationship with importance of spatial context of alternative habitat	(Sheaves 2005)

2.4.2 Context and habitat provisioning

The tendency for a habitat type, such as a type of vegetation or physical structure, to provide appropriate habitat resources and services for fish is dependent on context. For example, gradients in abiotic conditions lead to the exclusion of fish from some areas where there is otherwise suitable habitat (Akin et al. 2005, Ludsin et al. 2009). In these cases, a habitat type cannot provide suitable habitat simply because it cannot be inhabited, such as if there is not enough oxygen for fish to respire (Mattone and Sheaves 2017). This effect is evident for a range of different physical factors (Table 2.1, physical context). An important habitat function is the provision of appropriate food resources. This can be heavily context dependent, shaped by factors such as nutrient availability, which regulates primary productivity (Paerl et al. 1999) and secondary production (Gillanders and Kingsford 2002, Hoover et al. 2006). Interspecific competition can also alter habitat relationships by excluding certain species. Fish species that would otherwise use a wide range of habitats may be restricted to particular habitats in the presence of competitors (e.g. Hixon 1980, Hesthagen and Heggenes 2003). Often related to fish size (Hughes 1992, Webster and Hixon 2000), these dominance hierarchies can restrict the resources that are used by fish and the way they are accessed (Nakano 1995, David et al. 2007). The provisioning of complex nursery ground functions is highly context dependent, and often relies on functions or resource subsidies derived from areas well outside the habitat types where an individual is found (Litvin et al. 2018).

2.4.3 Spatial and temporal factors

The distribution of animals and habitats themselves throughout space and time can determine habitat relationships. For instance, most habitat relationship models assume that suitable habitat is saturated, but this will not always be the case (Fielding and Bell 1997). At low densities of the focal animal, a habitat patch may not provide its expected function simply because there are no individuals in the local environment to use it. On the other hand, during periodic, seasonal, or ontogenetic population bottle-necks, optimal habitat may become fully saturated, and other habitats will be used by individuals. For example, due to priority effects during larval settlement, optimal habitat may become fully occupied by early recruiters or adult residents (Ritter 2017), and remaining recruiters are left to occupy under saturated, suboptimal or non-preferred habitats (Almany 2003). Similarly, if a habitat type is scarce in the local seascape, fish may satisfy their requirements with alternative habitats. Where mangroves and seagrass are scarce at scales relevant to fish life-histories, some species, thought to be dependent on these habitats as nursery grounds, instead use appropriate microhabitat on reefs (McMahon et al. 2012). These effects can also occur at scales relevant to daily home ranges, where relative proportions of habitat appear to play a major role in determining habitat relationships (Huijbers et al. 2007). Similarly, the seascape context of the habitat patch itself is crucial in determining how that habitat is used by fish. The relationship between a species and a habitat type may be dependent on patch size, configuration, or the presence of other habitats in the surrounding seascape (Table 2.1, spatial context).

The use of a habitat by a fish is often influenced by the relative value of that habitat. Absolute qualities may be less important than relative qualities in relation to surrounding habitats. For

example, an important function of many habitats is the provision of appropriate food resources. The importance of this function for any given habitat is dependent upon the context of general availability of appropriate food, and the relative abundance and quality of the food in one habitat compared to other habitats in the local seascape. Pulses of prey, for example, can temporarily alter habitat relationships while consumers exploit a temporary resource. Habitats that seem generally important (even when inhabited for the majority of the time) may not serve important food provisioning functions. These changes in food resource context may be difficult to observe if temporally acute, and may lead to a skewed understanding of habitat function (e.g. Baker and Sheaves 2009b, a). In addition, the distribution of predators and food resources in space and time can interact strongly in determining habitat use (Houston et al. 1993, Heithaus and Dill 2002, Hoare et al. 2004).

The distribution of abiotic and ecological gradients throughout space and time can also determine habitat relationships. Unfavourable physical conditions can preclude an area from functioning as appropriate habitat (Sheaves 1996, Sheaves et al. 2007), and gradients or patchiness in unfavourable conditions is necessarily going to affect how fish use habitats in their aquatic landscape (Marshall and Elliott 1998, Zhang et al. 2009). The range of conditions experienced over time in a location, including the amplitude and frequency of fluctuation in conditions, can also determine the useability of a habitat – a habitat may lose its value for fish if conditions are sub-optimal even for a very brief period. Alternatively, when gradients in physical conditions vary temporally, fish fauna may only be able to access certain habitats at certain times. The time scales involved can be relatively brief, such as the periodic exposure of an intertidal habitat during low tide, or can span yearly cycles, such as the seasonal closure of estuaries (Lill et al. 2013) or the inundation of coastal floodplain-

wetlands (Mitsch et al. 2010). Connectivity pathways and features can change dynamically, such eddies and alongshore jets, constantly altering connectivity between habitats (Watson et al. 2012). Variation in availability of habitat has several consequences for habitat function (Table 2.1, temporal context), the most important being that the requirements fulfilled by a habitat when available must be fulfilled by an alternative habitat when it is unavailable. This necessitates animal movements and sometimes the use of multiple habitat types, enforcing the importance of spatial factors (Sheaves 2005).

2.5 Operationalising context

Fish-habitat relationships appear to be sensitive to a wide range of contextual factors. This implies that we are unable to broadly generalise any models of fish-habitat relationships beyond the spatial and temporal locations in which they were developed. The ample information available on the response of fish-habitat relationships to particular contextual factors demonstrates the non-transferability of these models. Without a detailed understanding of the relative importance of different factors, and interactions between them, this list of responses (Table 2.1) does not provide a basis with which to understand the limits of our models of fish habitat use.

I propose a general heuristic approach to the problem of context-dependence in ecology (Figure 2.2). Trying to define and understand the mechanistic relationships involved in context-dependence for a given phenomenon within a complex system is, most of the time, simply not possible (Harris and Heathwaite 2005, Harris and Heathwaite 2012).

Acknowledging uncertainty in the actual pathways of cause and effect, and instead focusing on delineating accurate boundaries and ranges for our knowledge, allows us to overcome complexity and produce useful understanding. By investigating a phenomenon in a range of different contexts, we can construct a *contextual distribution* of that phenomenon that more accurately represents the range of variation found in nature. Then, by identifying contexts under which that phenomenon predictably differs, we can build a list of contextual factors that are important to that phenomenon. By testing our predictions, we can find errors, which can identify different axes of context we did not previously consider. We can then re-define and re-predict, learning from our predictive errors across varied contexts. Finally, investigating each factor to determine the range within which the phenomenon occurs will allow us to define the contextual boundaries of certain outcomes.

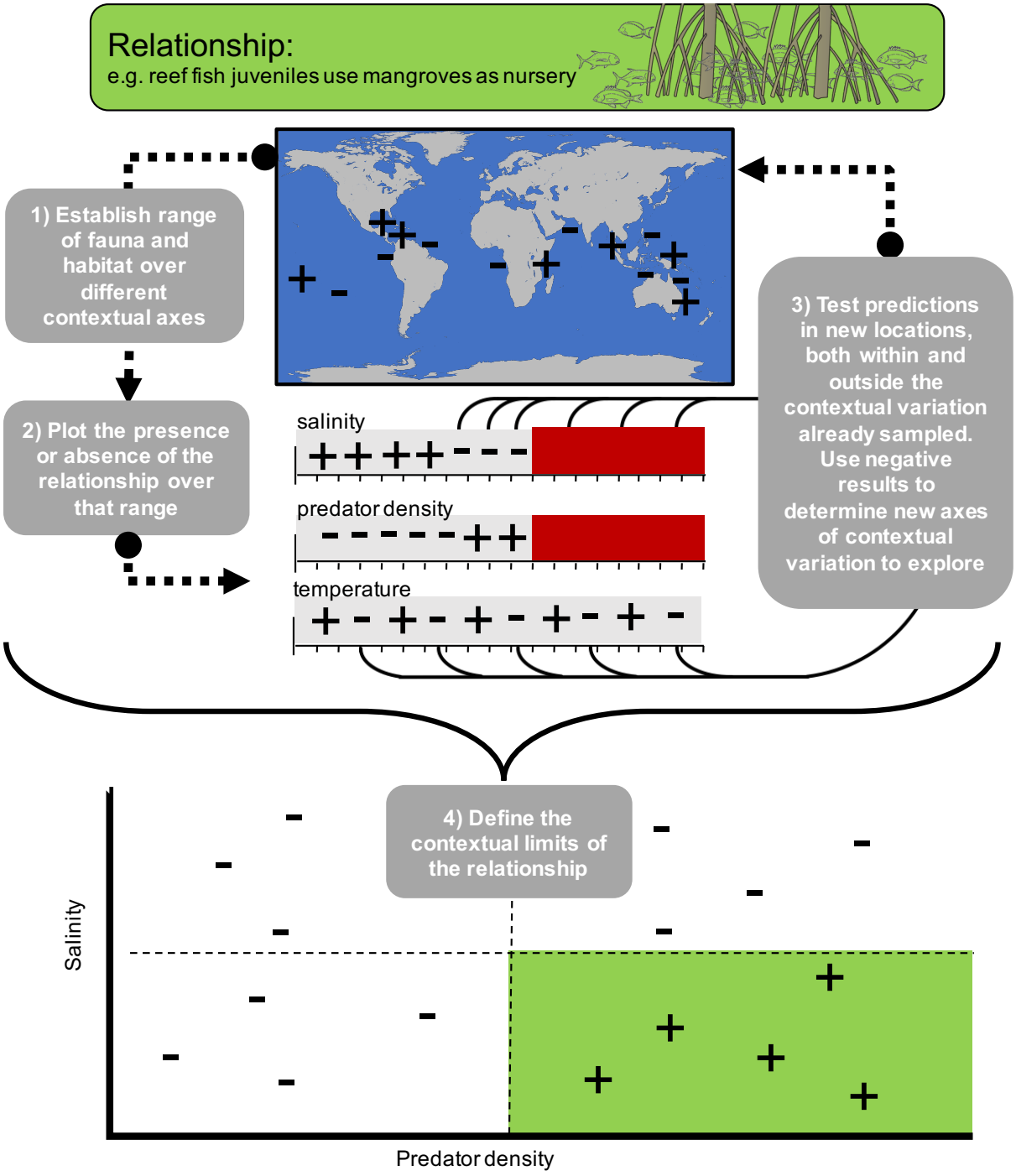


Figure 2.2 Schematic illustration of a heuristic process for determining context dependency in habitat relationships.

"+" indicates a field study where the relationship was found, "-" indicates a field study where the relationship was not found. The distribution of negative results indicates where the contextual boundaries of the relationship could be drawn in contextual space (bottom graph, dotted lines). For further details see section 6. *Operationalising context*.

Directly studying context-dependence provides a yardstick to establish the spatiotemporal relevance of fauna-habitat relationships and produce useful, usable knowledge. Establishing quantitative, measurable boundaries around relationships will require sustained, systematic research effort, along with broad syntheses of that effort. What are the advantages of this approach? Past research has identified particular elements of context relevant to fauna-habitat relationships, and responses to these particular elements. The concept of context provides a framework with which to integrate the effects of all known factors into a unified understanding of a particular relationship. This allows for the evaluation of relative importance of different factors in determining the outcomes, and an understanding of the interplay of these different factors.

2.6 Understanding regional differences in terms of context-dependence

How might context-dependence in habitat relationships play out over large geographic scales? If there is context-dependence in a relationship, then the range of contextual variation found within a region will partly determine the range of variation in the relationship in that region. There tend to be a few large-scale determinants that broadly characterise regions by constraining the range of variability in important contextual factors ('system level constraints' sensu Harris and Heathwaite 2012). I propose the term '*setting*' as a useful label for this small group of large-scale factors that define the range of contexts that exist within an area. For example, in a very low rainfall setting, lack of freshwater run-off will mean that brackish estuarine contexts will not be common – the range in salinity will be small, and average values will be high. By understanding the range of contexts that occur in different regions, we

can also predict differences in context-dependent habitat relationships between them. Therefore context-dependence could help explain broad, regional differences in the use of certain habitats (such as those in Kritzer et al. 2016). Three important determinants of setting for coastal fauna are tides, rainfall and geomorphology. These interact to determine the kinds of environmental contexts that are possible (Figure 2.3).

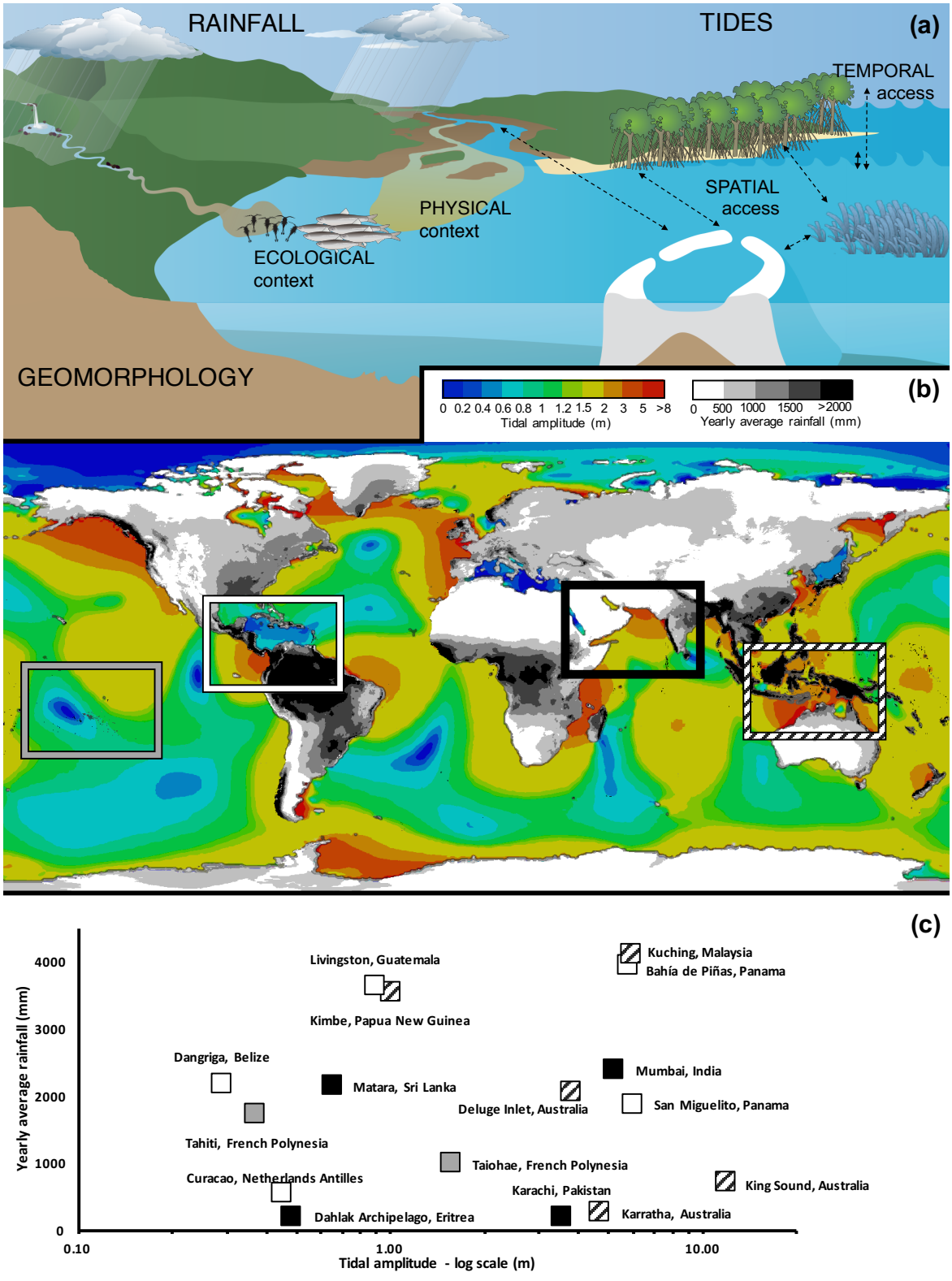


Figure 2.3 The impact of variation in tidal and rainfall regimes on the context of coastal aquatic habitat, and their variation across the globe.

Figure 2.3 caption continued: Top panel (a): Examples of how major modifiers of context for coastal aquatic habitats – tidal regime, geomorphology and rainfall regime – can interact in the landscape to modify context through their effects. Geomorphology and rainfall can interact to determine the physical and ecological context of coastal habitats by modifying the volume, pathway and composition of terrestrial run-off, which in turn modifies primary and secondary production, while geomorphology and tidal regime can interact to determine spatial and temporal access to coastal habitats through inundation regimes and the spatial arrangement of habitats. Middle panel (b): Tidal regime is shown for the oceans, and yearly average rainfall for the land, to illustrate how the two vary in coastal areas globally. Grey-scale intensity on land shows yearly average rainfall, while colours in the ocean show tidal amplitude (Tidal data from www.aviso.altimetry.fr and the National Tidal Centre, Australian Bureau of Meteorology, Rainfall data from WorldClim (Fick & Hijmans, 2017)). Bottom panel (c): locations from within boxes in *(b)* plotted in contextual space illustrate the spread of contextual variation within regions. Point colour patterns correspond to the regional box patterns in *(b)*.

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2.6.1 Tides

Tidal setting appears to predictably change the function of certain coastal habitat types, due to its profound effect on physical factors, species interactions, movement and connectivity pathways, and spatial and temporal elements of context (Krumme 2009). Tidal setting determines water movement, in terms of both magnitude and directionality. This directly changes the physio-chemical attributes of water column (Table 2.1, physical context). For instance, depending on tidal height and tidal phase, the intrusion of marine salinities inland and upstream into otherwise brackish habitats can vary. In addition, water movement can also change both feeding mode and type of habitat use, particularly the requirement for structured habitat, and timing of habitat use (Table 2.1, physical context – water movement). In intertidal and adjacent subtidal areas, tidal regime regulates the temporal availability of certain habitats by controlling access (Rozas 1995, Minello et al. 2012), and in some animals creates the requirement for certain spatial contexts, where habitats used at high tide and those used at low tide are present at appropriate scales (Sheaves 2005). Tides display extreme variation globally in three main dimensions; tidal range, frequency of flooding and duration of flooding (Pugh 1996), all of which can vary even at relatively small geographic scales.

These differences interact with local geomorphology, leading to fine-scale changes in the inundation patterns of coastal intertidal habitats (Baker et al. 2015) with predictable influences on habitat function (Baker et al. 2013). In higher latitudes, the range of habitat functions provided by saltmarsh can be heavily dependent on tidal regime (Raposa and Roman 2001), particularly nursery function (Minello et al. 2012). The situation is mirrored in tropical regions (Igulu et al. 2014) in the nursery function of mangrove forests and seagrass beds (see Section 2.7).

2.6.2 Rainfall

By determining terrestrial run-off, rainfall patterns are another key modifier of context (Gillanders and Kingsford 2002). Freshwater input changes the physical context in certain parts of the coastal zone, lowering salinity and increasing sediment loads, leading to turbidity in the water column and changes in nutrient availability, all of which can alter habitat relationships directly (Table 2.1, physical context) and indirectly by modifying species interactions, such as the quantity and type of food available to fish as well as their predator environment (Table 2.1 ecological context). In extreme cases, flooding can make coastal habitats intolerable places for fish, by creating intense high flow situations and intense oxygen depression (O'Connell et al. 2000), requiring successional recolonization by nekton (Thomaz et al. 2007, Gomes et al. 2012). Flooding also changes the dimensionality of the landscape. In channels, the water column increases in height relative to the benthos. This change in vertical dimension has a range of consequences for fish, such as allowing access for larger, deeper bodied animals (Sheaves et al. 2007a, Sheaves and Johnston 2008). If floodplains are inundated then the area of aquatic landscape is increased horizontally, playing

an important role in hydrological connectivity (Davis et al. 2012, Couto et al. 2017). The life-history strategies that combine the use of both freshwater and marine habitats require freshwater flow, which is scarce in areas with low rainfall, a mechanism thought to be responsible for South Africa's lack of diadromous fish species (Bruton et al. 1987). In areas where high rainfall causes flooding, a terrestrial grassland or forest can be habitat for fish (e.g. Copp 1989) – an impossible situation in low rainfall areas, where all habitat available to coastal fishes is essentially marine. This has important implications for barramundi (*Lates calcarifer*), which typically use both freshwater floodplains as well as freshwater rivers and pools during its life history (Russell and Garrett 1983, 1985). However, it can also rely on entirely marine nursery habitats in low rainfall areas (Pender and Griffin 1996, McCulloch et al. 2005). Therefore, in some areas the importance of marine habitat in providing a nursery function for juveniles may be far greater than in areas where diadromy is possible. It is not simply the freshwater flow itself that matters, but the context of reliable freshwater flows that leads to the evolution of processes, like trophic structures and behaviours, that harness these flows (Sheaves et al. 2007b).

2.6.3 Geomorphology

Geomorphology interacts with both tides and rainfall to determine the patchwork of coastal environments available to fish, and how they can be accessed. Geomorphology can determine rainfall through orographic effects, as well as determining how that rainfall proceeds to the ocean, and the resulting coastal aquatic landscape available to fish. For example, in steep volcanic landscapes, water runs off rapidly in channels, whereas in limestone landscapes, water percolates through to ground water, creating few rivers. Alluvial terraces produce slow

flowing riverscapes and wetlands, whereas on steep islands, fast flowing channels run directly into the marine environment. This can determine the type of life-history habitat use strategies that fish employ (Jones et al. 2017). These geomorphic features can drive the abiotic and biotic context of the landscape (Lee 1999). For example, in deep areas with little flow, temperature can increase and oxygen levels may drop, whereas in areas with rapid flow from upstream, temperatures may be lower and oxygen levels higher. The nature of terrestrial runoff can have a range of consequences for habitat context, and studies have linked geomorphology to the dominance of different habitat forming biota and key ecosystem engineers (such as coral and macroalgae) through nutrient availability mechanisms (Birkeland 1982, Littler et al. 1991) – determining the range of habitats available to fish, and their temporal stability. In a similar way, geomorphology determines the pathways of incoming tidal flow, modifying its strength and height, how long it remains in intertidal areas, and how it proceeds back to the ocean.

2.7 Mangroves as nurseries for coral reef fish: a case study in context-dependence

Our framework for determining context-dependence (section 2.5) provides a useful way to consolidate past work on particular phenomenon and direct future research. The notion that mangroves provide a nursery function for coral reef fish (Nagelkerken et al. 2000c, Nagelkerken and Van der Velde 2002), while certainly applicable to the contexts in which these foundational studies were carried out, has been generalised in conservation literature (e.g. McLeod et al. 2009). Mangrove plants occur over a wide range of contexts globally – they have adapted to exploit many kinds of substratums and environments (Duke et al. 1998,

Giri et al. 2011). Plagued by exceptions (e.g. Dorenbosch et al. 2009, Barnes et al. 2012, Sheaves et al. 2016) the prevalence of mangroves as coral reef fish nurseries seems to be highly variable and location specific. Using what is now a large body of relevant field studies, Igulu and colleagues (2014) were able to perform meta-analyses on the distribution of this phenomena. Tidal amplitude and salinity were found to be major drivers behind this relationship, regardless of biogeographic region. Specifically, small tidal ranges and higher salinity levels seem to drive the function of mangroves as nurseries for coral reef fish. Larger tidal ranges render mangroves inaccessible during low tide and complicate their utilisation by fishes (Sheaves 2005), who risk acute predation pressure during their daily forced migrations to appropriate subtidal habitats (Jelbart et al. 2007). Lower salinities would require otherwise entirely marine fish to have energetically expensive osmotic adaptations during early life history (Kültz 2015). In addition, if low salinities are experienced in mangrove habitat, it is unlikely that corals occur in close proximity as they are sensitive to fresh water and sedimentation (Rogers 1990).

The next step in this endeavour is to delineate the range within which mangroves perform this function along the axes of these two contextual factors. At what specific salinity levels and tidal ranges do mangroves cease to perform this function in a significant way? Are these factors themselves responsible for altering the function of mangroves, or are they useful proxies for other mechanisms? To refine our understanding, we require field studies spread across a wider range of contexts (Figure 2.3). The use of mangroves by juvenile reef fish has been well studied in the tropical Western Atlantic and particular locations in the Indo-Pacific (Berkström et al. 2012). Consequently, our understanding of this phenomenon is largely restricted to high salinity micro-tidal contexts, and low salinity meso-tidal contexts. There is

a paucity of field data from low salinity micro-tidal contexts such as the Coral Triangle (Olds et al. 2013), low salinity macro-tidal contexts such as those found in the Tropical Eastern Pacific and Western Atlantic (Castellanos-Galindo and Krumme 2013, Castellanos-Galindo and Krumme 2015) and high salinity macro-tidal contexts (e.g. the north-western coast of Australia). In this endeavour, both positive and negative findings are of equal value, and both new field studies and negative results not published as nursery ground studies could prove useful.

2.8 Conclusion

As our impact on the biosphere continues to accelerate, and the countless services provided by ecosystems are undermined, nations and organisations scramble to preserve, restore or enhance important habitat functions. Global climatic change promises large shifts in many aspects of context (Stenseth et al. 2002). In order to predict actual impacts, we must develop knowledge of context-dependence in the complex networks of interactions that maintain ecological communities (Tylianakis et al. 2008). Our ability to forecast and anticipate how habitat functions are altered are an integral part of our adaptation response (Metcalf et al. 2013). Without the ability to establish the limits of our knowledge of habitat relationships, we risk the failure of ecological science to provide useful information where and when it is most needed.

3 Remote underwater visual census methodology

The biological data presented in the main body of this thesis was collected using a single technique, unbaited video point census surveys. Here, I provide justification for the use of this technique, a description of the methodology and justification of the metrics derived from the technique. The following section includes heavily expanded excerpts from the published version of Chapter 4 (Bradley et al. 2019), which I have removed from that chapter to avoid repetition in the thesis.

3.1 Data requirements

The driving focus of the research presented in this thesis is to identify variability in fish-habitat relationships across a range of different environmental contexts. This focus imposes the somewhat novel requirement that data collected in different environmental contexts must be directly comparable. Previously, our ability to understand variability in fish habitat use has been hindered by a lack of comparable data. On coastlines with significant terrestrial run-off, fish communities are typically investigated using a range of non-comparable techniques. Traditionally, marine habitats have been surveyed using visual census by divers (Barnes et al. 2012). The disturbance associated with divers or ROVs often triggers a flight response in fish (Thompson and Mapstone 1997, Stoner et al. 2008), so in more turbid areas, visual census by divers is inviable because the flight distance can often be greater than the range of visibility.

In addition, in many estuarine areas diver surveys are not possible because of large predators (e.g. crocodiles) or extreme currents. Instead, soft bottom estuarine habitats have been surveyed with trawling methods (Rozas and Minello 1997), and structured estuarine habitats, such as mangroves, have been surveyed indirectly with netting techniques (Sheaves et al. 2012). Consequently, it has been difficult to compare habitat use and assemblage structure both between different habitats types in estuarine environments, and between estuarine and marine habitats. Furthermore, studies conducted in different regions are often conducted by different research teams using different methodologies. These methods have often been developed somewhat independently, to suit local conditions or data requirements. This limits our ability to empirically understand differences between regions, and differences in habitat use between contexts that vary between regions, such as climate and tidal regime.

In the research presented in this thesis, I use a single technique, low disturbance remote underwater video census, to characterise habitat use throughout the full range of shallow habitats available in a region, in both marine and estuarine contexts (Chapter 4), and in mangrove habitat across the Indo-Pacific (Chapters 5 and 6). The development of affordable, high quality underwater video units has been a major break-through in overcoming the problem of fish flight response in limited visibility situations (Sheaves et al. 2016), enabling ecologists to accurately define natural fish-habitat relationships in a range of inaccessible and challenging environments (Cappo et al. 2003, Bradley et al. 2017). This technology has allowed me to directly compare fish habitat use across different habitats and contexts for the first time.

3.2 Technique development

The low disturbance remote underwater video census technique employed in this thesis was developed through an extensive trial period preceding the doctoral candidature. To ensure representative and comparable data was collected in a range of different situations, a series of tests were carried out on the performance of video deployments under differing conditions, and the impact of cameras on the behaviour of fishes (Bradley 2013). Importantly, no substantial gear avoidance effects were found during these trials. The technique was subsequently peer-reviewed (Bradley et al. 2017), and has been used to validate the results of otolith chemistry and acoustic telemetry in describing the seascape use strategies of coastal Lutjanids (see Appendix D, a publication arising from the data collected as part of this thesis). It is now a commonly adopted technique for researchers working in similar coastal environments (Gilby et al. 2016, Gilby et al. 2018a, Gilby et al. 2018b).

3.3 Remote underwater video census methodology

3.3.1 Deployment protocols

Underwater cameras were fixed onto a metal frame during deployment for protection. These video units were deployed from a vessel, with a surface float for retrieval. Video units were designed to ensure homogeneity in camera orientation when remotely deployed (i.e. without being positioned manually). The camera was orientated horizontally at an angle of 0º and a

field of view of 130º, positioned at a height of 10 cm relative to the substratum. A patterned plastic strip was fixed 0.5 m from the lens in the camera's field of view to provide a standard measure of water clarity. Each deployment was >15 minutes, to ensure that at least 15 minutes of usable footage was captured.

Surveys were conducted during daylight hours and periods of relatively low turbidity to ensure conditions appropriate for video sampling. As baited cameras attract fish from surrounding areas, and my objectives were to describe small-scale fish-habitat relationships, these deployments were unbaited. The vessel was maintained >100 m from each camera for the 15 minute recording period to reduce the impact of boat presence on fish behaviour. Independence of video samples was maintained by spacing cameras at least 20 m apart, with most replicates 50-100 m apart.

3.3.2 Video processing

On review of footage, potential biases due to water clarity were reduced by only including videos above a minimum threshold of 0.5 m (i.e. when the patterns on the patterned strip 0.5m in front of the camera were visible). Similarly, not all footage from each deployment was viewed. While each deployment produced >15 minutes of footage, a single sample only consisted of 15 minutes of undisturbed footage; periods of disturbed sediment and boat presence immediately following deployment were discarded. Typically, this meant that the first minute was discarded due to boat presence, along with a subsequent period (the length of

which was heavily dependent on substratum type) where the footage did not meet the minimum visibility threshold of 0.5 m.

I identified fish present in each video sample to the lowest taxonomic level and life-history stage (juvenile vs adult) possible. Classification was based on colouration/shading patterns and body shape (Allen 1985, Wilson 1998, Allen et al. 2012, Froese and Pauly 2018). For taxa where there were clearly defined visual differences in these characteristics between recently settled individuals (e.g. weeks or months post-settlement) and older juveniles (e.g. years post-settlement), I divided juveniles into 'early' and 'late' phases. Identifications were reviewed by experts to ensure correct identification. Identifications where consensus could not be reached were assigned to the level of taxonomic grouping (e.g. genus) where consensus was achieved. Several taxa could only be identified to higher taxonomic levels because the characteristics that distinguish some species, such as fin ray counts or morphological measurements, could not be distinguished. In analysis, species were grouped to higher taxonomic levels when less than 80% of individuals could be positively identified to species level. When more than 80% were positively identified, I still only included positively identified individuals in analyses for that species. It was often impossible to identify early juvenile stage individuals in the genera *Siganus* and *Lethrinus* to species level. On the occasions where individuals of these genera swam within close range of the camera, positive identification to species level was possible, based on differences in juvenile markings. It was not possible to identify juveniles for the families Mugillidae, Clupeidae and Gobiidae. From each video, I extracted fish species/life-stage presence, and measured fish species/life-stage abundance using the maximum number of individuals seen within the field of view in any

single video recording frame (30 frames per second) over the 15 minute sample (MaxN), to avoid multiple counts of the same individuals (sensu Harvey et al. 2007).

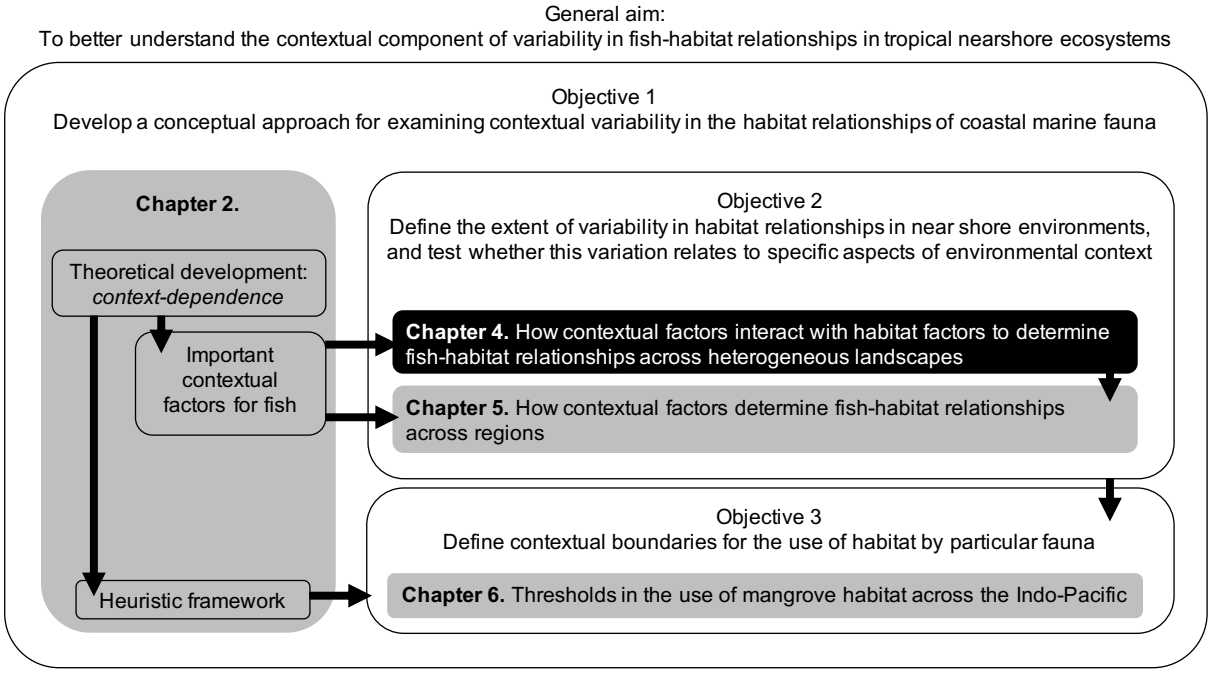
This technique has a number of specific strengths and limitations. The small size of the camera units, and the low disturbance method of deployment (gently lowered from a small vessel and then left undisturbed for 15 minutes), seems less likely to trigger avoidance by species sensitive to other methods such as diver surveys (Thompson and Mapstone 1997, Dickens et al. 2011). So while it is not possible to totally eliminate gear avoidance for any gear type, this method should provide the most accurate measure of assemblage. Due to the ease of deployment and the potential to simultaneously deploy multiple camera units, high replication is possible within a limited time frame. Working with footage also has a number of advantages over human observations (Cappo et al. 2003). Consistent identification is possible through expert review, and individual instances can be reviewed, and retrospectively corrected. However, as is the case with all visual methods, sampling cannot be carried out during periods of low visibility, limiting the temporal coverage that can be achieved with this technique.

3.4 Interpretation of data from remote underwater video census

Remote underwater video census provides a point census of the fish community, and a point assessment of biological and structural habitat characteristics. Predictor and response variables are captured at the same spatio-temporal scale, and with high replication, providing the information required to define fish-habitat relationships (Hannah and Blume 2012). When

conducted across habitat types or environmental gradients, it provides a relative measure of a species/life-stage habitat use with which to assess the response of that group to those habitat or environmental differences (e.g. Bradley et al. 2017, Gilby et al. 2018b).

4 Context is more important than habitat type in determining use by juvenile fish



Abstract

Habitat characteristics are often equated with habitat function for animals, but contextual factors can complicate these assumptions. In this chapter, I examine the potentially interactive structuring effects of local habitat characteristics and environmental context on assemblage composition. Specifically, I studied the habitat use patterns of juvenile fish throughout an entire region, where a diversity of structural habitat types exist in both estuarine and marine contexts. Until now, it has been difficult to determine the full breadth of habitat use by juvenile fishes due to the array of gear types used in different situations. I used a single technique - remote underwater video census - to explore the importance of habitat type (biotic structural components, substratum, and depth) and environmental context (marine versus estuarine) in structuring juvenile fish assemblages. The 1315 video surveys collected show a clear hierarchy in the organisation of juvenile fish communities, with assemblages being first distinguished by environmental context, and then by habitat type. Marine and estuarine mangroves contained entirely different assemblages, and likewise for rocky reefs and submerged aquatic vegetation. Many juveniles were found in multiple habitats within each environmental context, and some appear to shift between habitats as they grow. This suggests that two functionally different 'seascape nursery' types exist at local scales within a single region, defined by their context. These results provide clear evidence of the importance of context-dependency in animal-habitat relationships. They show that the context of a location can be of far greater significance in determining its potential habitat function than what habitat-forming biota and substratums are present, and stress that apparently similar habitat types occurring in different contexts may be functionally distinct. This study highlights that a robust understanding of context must be considered before equivalent habitat function can be assumed with confidence.

4.1 Introduction

Habitat characteristics (such as vegetation type) have long been recognised as the key determinant of animal communities throughout land and seascapes (Southwood 1977). Accordingly, the habitat characteristics of a location have long been equated with the functional role of that habitat for animals. However, ecologists have recently started to examine how context can influence the assemblage of animals found in certain habitats. Physical context (e.g. Bellwood et al. 2002), ecological context (e.g. Laundré et al. 2010), spatial context (e.g. Turner 1989), and temporal context (e.g. Law and Dickman 1998), all modify the way habitats are used by animals. Thus, together, habitat characteristics and contextual factors interact to determine the distribution of animals (Sisk et al. 1997). Local habitat characteristics tend to be consistently important predictors of animal presence, while contextual factors are usually only important when considered in combination with local habitat characteristics, and their importance tends to vary according to the taxa and system under investigation (Mazerolle and Villard 1999, Atauri and de Lucio 2001). Understanding both the relative importance of these factors, and how they interact, is essential for understanding how animals are causally linked to their environment, and how they might respond to change.

For some systems and taxa, we still do not have a systematic understanding of how contextual and local habitat factors interact to determine the distribution of animals. On many coasts, a suite of similar habitat types are present across a patchwork of marine and estuarine contexts, often in quite close proximity. Seagrass meadows, for example, can occur anywhere from enclosed low-salinity swamps to the seabed of the continental shelf, including bays and

reefs in between (Carruthers et al. 2007). Studies have rarely explicitly tried to encompass the full breadth of variation present in these contextually heterogeneous regions, despite the fact that many fauna have the potential to use both marine and estuarine environments (Able 2005). This raises the question: do animals relate to these habitats across their full range, or are their habitat relationships context dependent? And, if so, how do habitat characteristics and contextual factors interact to determine assemblages in these regions? This remains a large and critical gap in our understanding (Faunce and Layman 2009, Sheaves 2017).

For juvenile fish, developing a detailed understanding of habitat relationships in these contextually heterogeneous regions is particularly important. The juvenile phase in the life cycle can be a critical population bottleneck (Chambers and Trippel 2012) and during this period, growth and mortality can be mediated by habitat (Tupper and Boutilier 1997, Grol et al. 2014). This can lead to complex habitat requirements. A common Caribbean reef fish, *Haemulon flavolineatum,* shifts between rubble, seagrass, mangroves and boulders to optimise survival and growth during its juvenile phase (Grol et al. 2014). Accordingly, the availability of appropriate juvenile habitats can have strong impacts on populations of adults (Nagelkerken et al. 2017). Knowledge of habitat use by juvenile fish is used to assign functional nursery roles to particular habitat types, such as mangroves or saltmarsh (Whitfield 2017). Thus, knowledge of habitat use by juvenile fish underpins efforts to conserve species and sustain fishery production (Crowder et al. 2000, Nagelkerken et al. 2012).

The influence of terrestrial run-off and the different contexts its presence or absence creates, is a considerable source of potential variability in habitat use (Kimirei et al. 2015, Whitfield and Pattrick 2015). The use of incomparable techniques to sample fish-habitat relationships

in these different environments has limited our ability to understand the interplay of habitat and contextual factors along heterogeneous coastlines (as discussed in Chapter 3, Section 3.1). Here, I employ a single method, low disturbance remote underwater video census (Chapter 3, Section 3.3) to characterise juvenile habitat use throughout the full range of shallow habitats available in a region, in both marine and estuarine contexts. My study area provided natural experimental conditions with a diversity of structural habitat types present in both estuarine and marine areas. I used machine-learning analysis to observe non-linear relationships and complex interactive effects between factors. Here, I examine how local habitat characteristics and context contribute to the organisation of assemblages throughout an entire region, to understand the interplay of these two factors in heterogeneous coastal environments.

4.2 Material and Methods

4.2.1 Study site

Sampling was carried out between 2012 and 2015 in the Hinchinbrook region (18˚ S, 146˚ E), off north eastern Australia (Figure 4.1), which encompasses areas of the mainland, as well as Hinchinbrook Island and the Palm Islands. Hinchinbrook Island lies adjacent to the mainland separated by a channel which contains a diverse mosaic of habitats. Terrestrial run-off from two rivers and many small creeks produce seasonal and daily variations in salinity (Wolanski et al. 1990). This large estuarine channel consists of mangrove forest, intertidal sand and mud flats, and sub-tidal rocky boulder fields, biogenic soft bottom and vegetated habitats (Alongi

et al. 1998, Bradley et al. 2017). By contrast, the eastern coast of Hinchinbrook island (i.e. ocean-facing side) is composed of extensive sandy flats, smaller creeks, as well as non-estuarine bays and fringing coral reefs. The Palm Islands lie 15 km offshore, and do not experience significant variations in salinity. This near-shore complex of 10 continental islands, contains a diverse mix of intertidal mangrove forest, reef flat with areas of live coral, rubble, seagrass, macro-algae and unvegetated sand, subtidal boulder fields, and extensive fringing coral reefs.

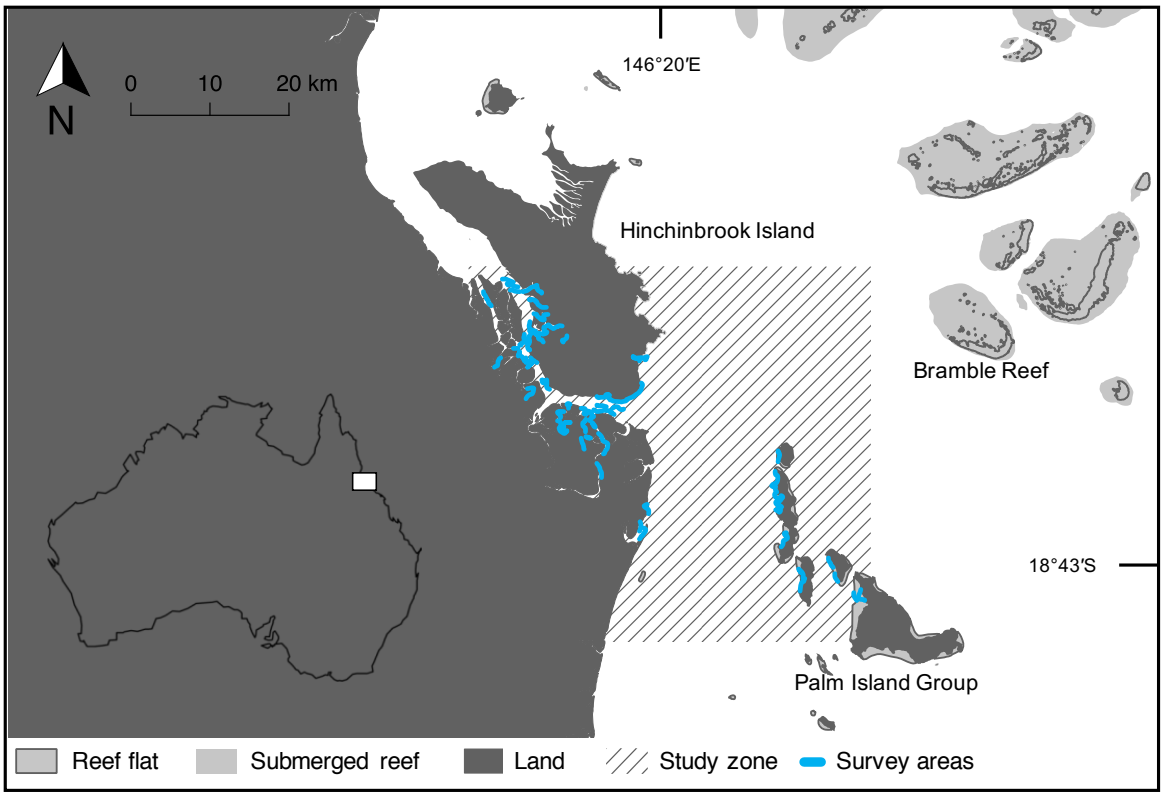


Figure 4.1 Location of the Hinchinbrook/Palm Islands region in north eastern Australia, and the areas covered by video point census surveys

The study region contains almost the entire breadth of coastal and nearshore benthic habitats commonly available to fish species in north eastern Australia (Sheaves 2009), allowing the diversity of habitat variation to be encompassed without confounding among-habitat

differences with faunal differences among regions. Accordingly, any differences in species-specific juvenile presence between habitat types can be more reliably attributed to physical, geomorphic and biological factors at the habitat patch scale, rather than at the oceanographic scale, and are not due to latitudinal or climatic differences in species distributions.

4.2.2 Video surveys

Video sampling was carried out as per the methods described in Chapter 3, Section 3.3. Sampling occurred between June and December, outside the North Australian monsoon. The minimum water depth surveyed was 0.5 m, and the maximum water depth surveyed was 10 m. Sampling was carried out during the full breadth of variation in tidal inundation (max. tidal amplitude 3.9 m) both in terms of the tidal cycle (high-low) and tidal periods (springs and neaps). The depth of every deployment was determined by acoustic depth sounder. I distinguished estuarine from marine areas based on regular periodic fluctuations in salinity established by previously published research (Wolanski et al. 1990), ground-truthed at the time of video sampling by measuring salinity.

For each video sample I determined substratum texture and dominant biotic habitat, based on a visual estimate of what occupied the greatest percentage area visible in the field of view. Each sample was assigned a classification based on a scheme (Table 4.1) following Ball et al. (2006). This resulted in 20 different combinations of substratum and biota found throughout the region – giving 20 putative habitat types, of which some were commonly found, and others only rarely encountered (see Appendix A, Table AA1). By partitioning habitat

characteristics finely, I could observe the combination of characteristics that juvenile fish actually responded to in my subsequent analyses.

Efforts were made to sample the entire breadth of habitat variation present in the region. Initially, the study area (Figure 4.1) was sampled randomly, with cameras placed at random intervals from the shore, to achieve broad spatial replication. After reviewing the metadata, targeted sampling was performed to boost replication in substratum/biota combinations with low representation, though for some rare combinations of biota and substratum, this could not be achieved (see Appendix A, supplementary methods – survey design). The resulting 1,315 video samples, while not completely orthogonal, captured the broad variability in habitat across the depth range (0-10m) throughout the study zone (see Appendix A, Table AA1). While the resulting data set is not strictly stratified, differences in replication between habitat types are representative, and are accounted for by the analytical pathway detailed below.

Video footage was processed as per Chapter 3, Section 3.3.2. Both presence and abundance of each taxa/life-stage was used in the analyses detailed below. Abundance measured using MaxN is useful for understanding relative difference in the abundances between sampling locations for each taxa/life-stage group (as is produced in a Bray-Curtis distance matrix), whereas presence/absence information is useful for understanding differences in probability of encounter between different sets of samples.

4.2.3 Statistical Analysis

Rather than using some preconceived classification of nursery habitat types and analysing for differences in assemblage composition between them, I 'let the species tell their own story' (Field et al. 1982). I avoided a priori habitat categories by partitioning habitat characteristics finely, pooling all samples and employing a series of Classification and Regression Tree (CART) analyses. Juvenile presence and assemblage composition is used to identify habitat qualities that juveniles relate to, which is then used to define juvenile habitat types in an empirical way.

While all available habitats were surveyed extensively, samples from coral habitats were not pooled with the other data in my tree analyses, as coral habitat is known juvenile habitat for many reef fish species that do not utilise other potential coastal nursery habitats surveyed in this study (Dorenbosch et al. 2005, Honda et al. 2013). Following the classification used by Kimirei et al. (2011), I pooled shallow coral habitat from the crest, flat, and back-reef, and deeper coral habitat from the reef slope. As I was only interested in seeing if coral was an important juvenile habitat for those species using other juvenile habitats, for simplicity only species that had been encountered in other habitats as well are presented. The results of these reef surveys are presented alongside the results from the non-coral nursery habitats identified in the following analyses for comparison.

Firstly, to broadly examine the use of different habitats by juvenile fish, each video sample was given a binary classification according to whether any juveniles of any species were

present (1) or not (0). Univariate classification tree analysis was performed using the 'party' package in R (Hothorn et al. 2010), with habitat characteristics (a single identifier combining dominant biota and substratum texture – see Table 4.1) as the predictor variable. The resulting tree presents the significant differences in the data set based solely on habitat, and the p-values associated with each split. This allowed us to distinguish the habitat types where juveniles were usually present (juveniles found in >70% of samples) from the habitat types where juveniles were usually absent (juveniles found in <30% of samples), regardless of their estuarine or marine context.

Secondly, of the habitats where juveniles were usually present, I sought to determine which predictor variables were linked to differences in juvenile fish species composition by using multivariate regression tree analysis. The univariate tree had identified several habitat categories where, throughout the region, regardless of estuarine or marine context, juveniles were usually absent (juveniles found in <30% of samples). Multivariate distance measures tend to behave erratically when many sparse samples are included in analysis (Clarke et al. 2006). Habitat types where less than 30% of samples contained juveniles were excluded, to allow the multivariate analysis to identify patterns of juvenile presence rather than being overwhelmed by zeros due to species absences. The data for these excluded habitat types is presented along with the juvenile habitat types for comparison (see Appendix A, Table AA2). For the same reasons, I removed all videos where no juveniles were present, and I ran the tree analysis using three different arbitrary decision rules to eliminate rare taxa: excluding taxa that occurred in <3%, <5% and <10% of samples. The same tree structure was returned for all three decision rules, indicating the structure was robust to all species that occur in >3% of samples. This is the final tree presented (Figure 4.3a). The multivariate regression tree

analysis was performed with Bray–Curtis dissimilarity as the distance measure, using the mvpart package in R (De'ath 2007, Ouellette and Legendre 2012).

Based on the predictors that best explained both juvenile presence and species composition, I defined six functionally different juvenile habitat categories (each of which combine several of the original finely partitioned habitat categories): shallow estuarine rocky reef, deep estuarine rocky reef, estuarine mangroves and woody debris, marine rocky reef, marine seagrass and macroalgae, and marine mangroves. Each category is defined by a distinct juvenile fish assemblage (Figure 4.3b). For each juvenile habitat defined I present presence/absence information for all species and life stages identified (see Appendix A, Table AA2). To examine differences in habitat use for common fish species, I calculated the individual probability of encountering each of the 16 most frequently encountered juvenile species in my data set (determined by presence, summed and ranked across all samples), in each juvenile habitat based on all data. I used approximate Bayesian computation in R to estimate the probability of encounter for each fish species life stage and estimate the uncertainty around that probability. For those common taxa where both early and late juvenile stages could be confidently distinguished, relative density was estimated for each juvenile stage in each juvenile habitat type. To estimate relative density, CPUE (Catch Per Unit Effort: MaxN per 15 minute video sample) was calculated for each habitat.

4.3 Results

4.3.1 Juvenile presence

Juveniles were observed primarily in structurally complex habitat rather than unstructured habitats. The 1254 non-coral fish-habitat video samples were classified into 20 different combinations of substratum texture and dominant biota during video analysis. Of these putative habitat types, four were identified in univariate tree analysis (based on presence/absence of any juveniles) as having consistently low occurrences of juveniles (<30% of samples) regardless of depth and marine or estuarine context (Figure 4.2). In three open bottom habitats (bare gravel, mud and sand) juvenile encounter was extremely rare (5.0%). In seagrass beds with muddy substratum, juvenile encounter was also low (28.6% presence). Assemblage analysis was then performed on the remaining samples containing juveniles (n = 417 video samples) from the 16 other putative habitat types where juvenile encounters were more common (>70%).

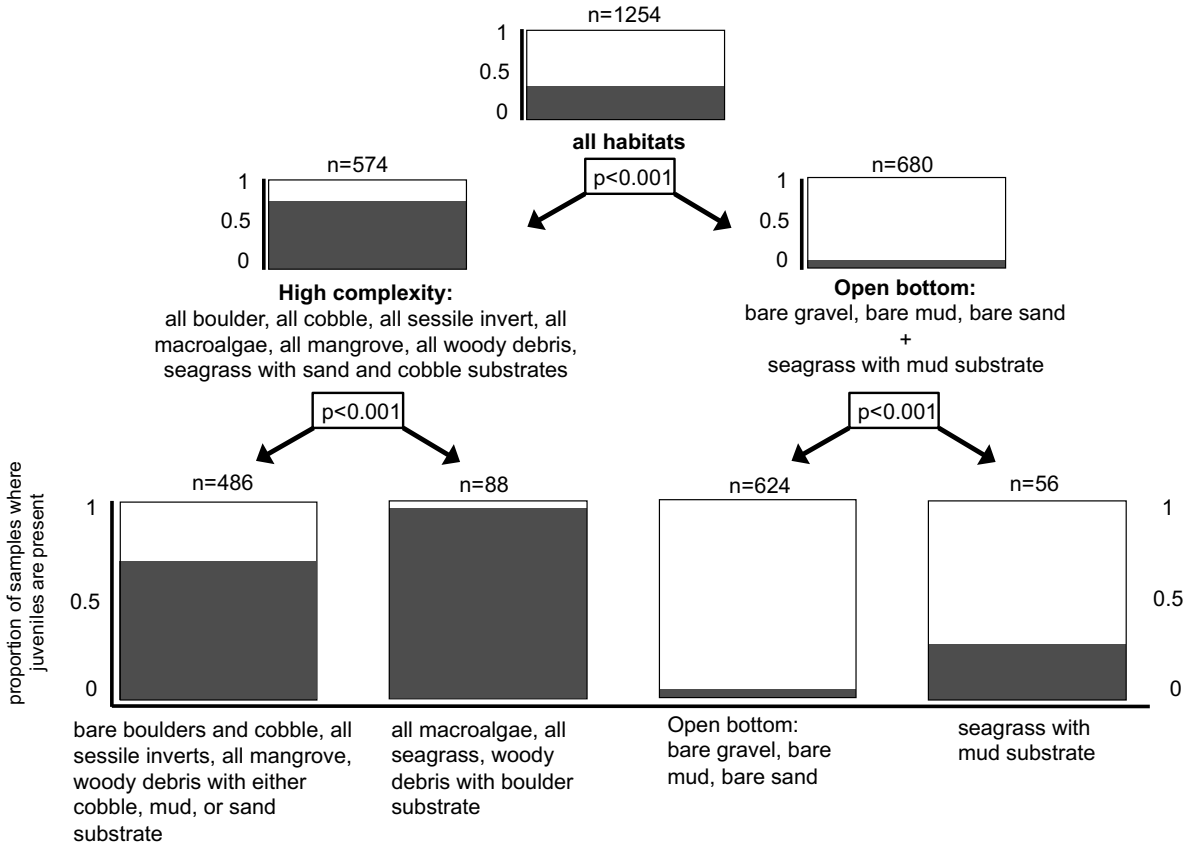


Figure 4.2 Univariate classification tree of the presence or absence of juvenile fish, performed on all non-coral samples (n = 1254).

Each division is labelled with the variable used in the split, the result of the significance test of the difference between the two groups separated by the split, and on either side of this label, the categories separated by the split. Black bars indicate the proportion of samples where juveniles were present in each terminal node. See Table 4.1 for explanation of habitat categories.

4.3.2 Juvenile assemblage composition

Multivariate analysis of fish assemblage composition showed a clear hierarchy in the organisation of juvenile fish communities, with assemblages being first distinguished by environmental context, and then by habitat type, lumping the 16 different combinations of habitat characteristics into six functionally dissimilar juvenile habitats (Figure 4.3a): shallow estuarine rocky reef, deep estuarine rocky reef, estuarine mangroves and woody debris, marine seagrass and macroalgae, marine rocky reef, and marine mangroves.

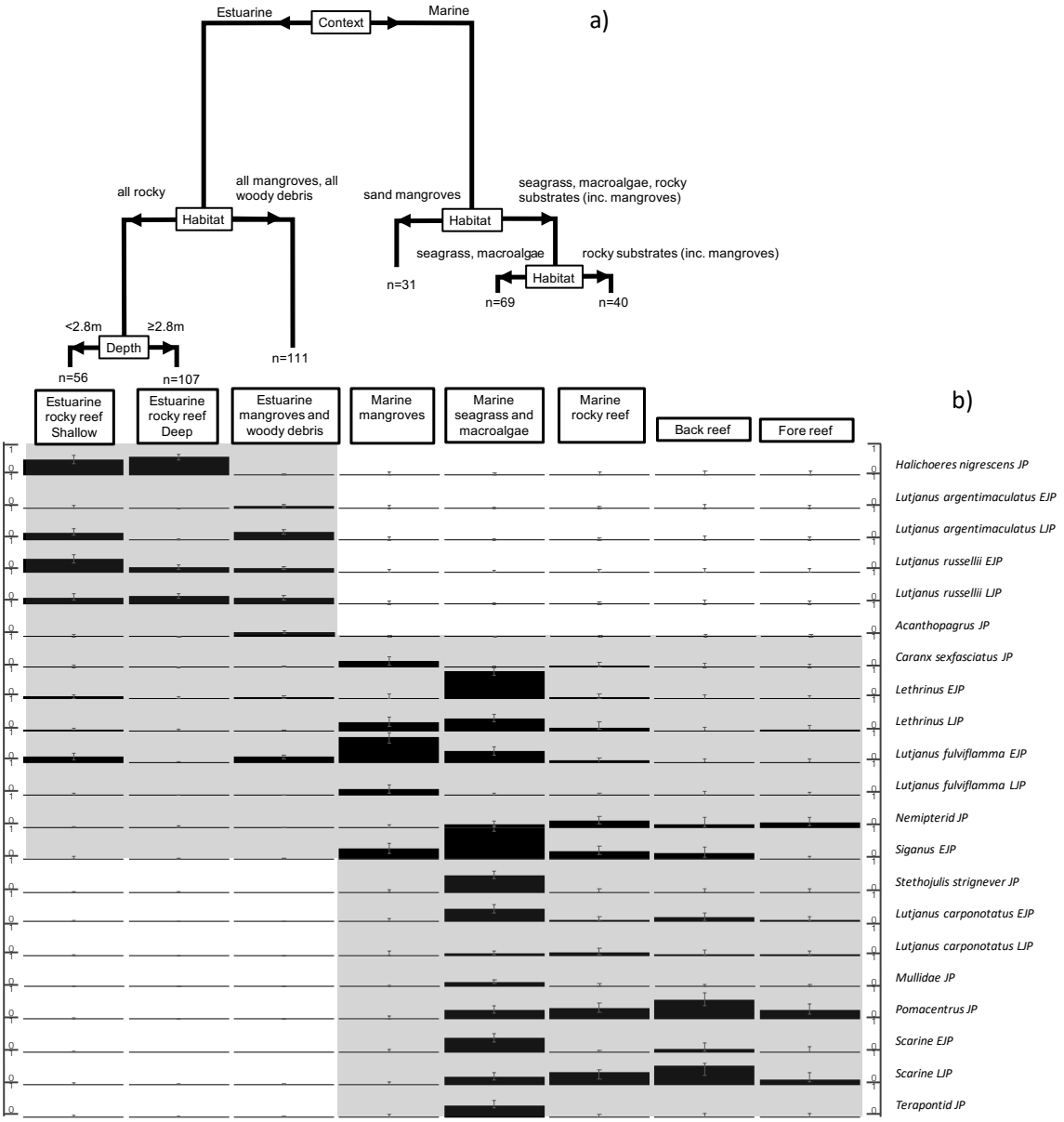


Figure 4.3 a) Multivariate regression tree showing the major divisions in juvenile assemblage composition throughout the region.

Analysis was performed on all samples from the 16 putative habitat types where juvenile encounters were >70%, excluding those samples where no juveniles were present (n= 417). Each division is labelled with the factor used in the split and the set of categories or values that are separated by the split. The distance of descending branches in the dendrogram is proportional to the difference between groups. b) Approximate Bayesian computation was used to estimate both the probability of encounter for each fish species life stage and the uncertainty around that probability. Histograms below each terminal node show probability of encounter with 95% confidence intervals for the 16 most commonly encountered juvenile taxa in shallow habitats of the Hinchinbrook/Palm Islands region. As histograms show modelled presences, error bars are sometimes visible even when there were no recorded occurrences – an encounter rate of zero in the data set does not necessarily mean a zero probability of encounter. Back and fore reef habitats are also displayed in this figure for comparison, though they were not included in the CART analysis. Taxa are ordered according to their presence in the six habitats (grey shading): species in the first 6 rows are only present in the three estuarine habitats, the second group (rows 7-13) are present in both the estuarine habitats and the marine habitats, and the third group (rows 14-21) are only present in the marine habitats. JP = (entire) Juvenile Phase, EJP = Early Juvenile Phase, LJP = Late Juvenile Phase

Multivariate regression tree analysis of video samples separated those from marine environments and those from estuarine environments (Figure 4.3a). Within these two environmental contexts, samples were split based on habitat attributes; however, the particular habitat attributes that made up important juvenile habitat differed between the two contexts (Figure 4.3a). Within estuarine contexts, the fish assemblage varied most between rocky habitats and mangrove or woody debris habitats, and the assemblage in rocky habitats also varied according to depth. Rocky habitats included samples that were bare, as well as those from rocky substratums with seagrass, macroalgae, and encrusting sessile invertebrates as their dominant biota. Within marine environments, the assemblage varied most between sandy mangroves and all other structured habitat, which then differed based on either the presence of submerged aquatic vegetation (seagrass and macroalgae), or rocky substratum. This last node included both bare rocky substratums, and rocky substratums with mangroves. The major difference in assemblage structure between the two salinity contexts is clearly illustrated by the probability of encounter of individual species among habitats across the seascape (Figure 4.3b). A set of taxa were only found as juveniles within estuarine contexts, including species from the families Lutjanidae, Labridae and Sparidae. Another set of juveniles were found across both estuarine and marine contexts, but were more frequently encountered in marine habitats. This included species from the families Carrangidae, Lethrinidae, Lutjanidae, Nemipteridae and Siganidae. A third set of taxa were only found in marine contexts, and included species from the families/sub-families Labridae, Lutjanidae, Mullidae, Pomacentridae, Scarinae and Terapontidae.

Locations with the same habitat characteristics harboured a completely different set of species depending on the marine or estuarine context in which they were found. Estuarine

mangroves contained an entirely different assemblage to marine mangroves, and likewise for rocky reefs, and submerged aquatic vegetation.

4.3.3 Habitat use patterns of early vs. late juveniles

Of taxa that were encountered in >3% of total samples, where both early and late juvenile phases could be identified, habitat use patterns were often different according to juvenile phase, but remained within either an estuarine or marine context (Figure 4.4). In general, early juvenile stages mostly occupied a single habitat type, and were found infrequently in other habitat types. By contrast, late juvenile stages were frequently encountered in 2-4 habitat types. In the marine environment, there was a trend of early juveniles in macroalgae and seagrass vegetated habitat, and late juveniles in the mangroves, rocky reef and back reef habitats. One exception to both these patterns is *Lutjanus fulviflamma*, which is found as an early juvenile in areas of both estuarine and marine salinities, and is found as a late juvenile almost exclusively in a single habitat type – marine mangroves.

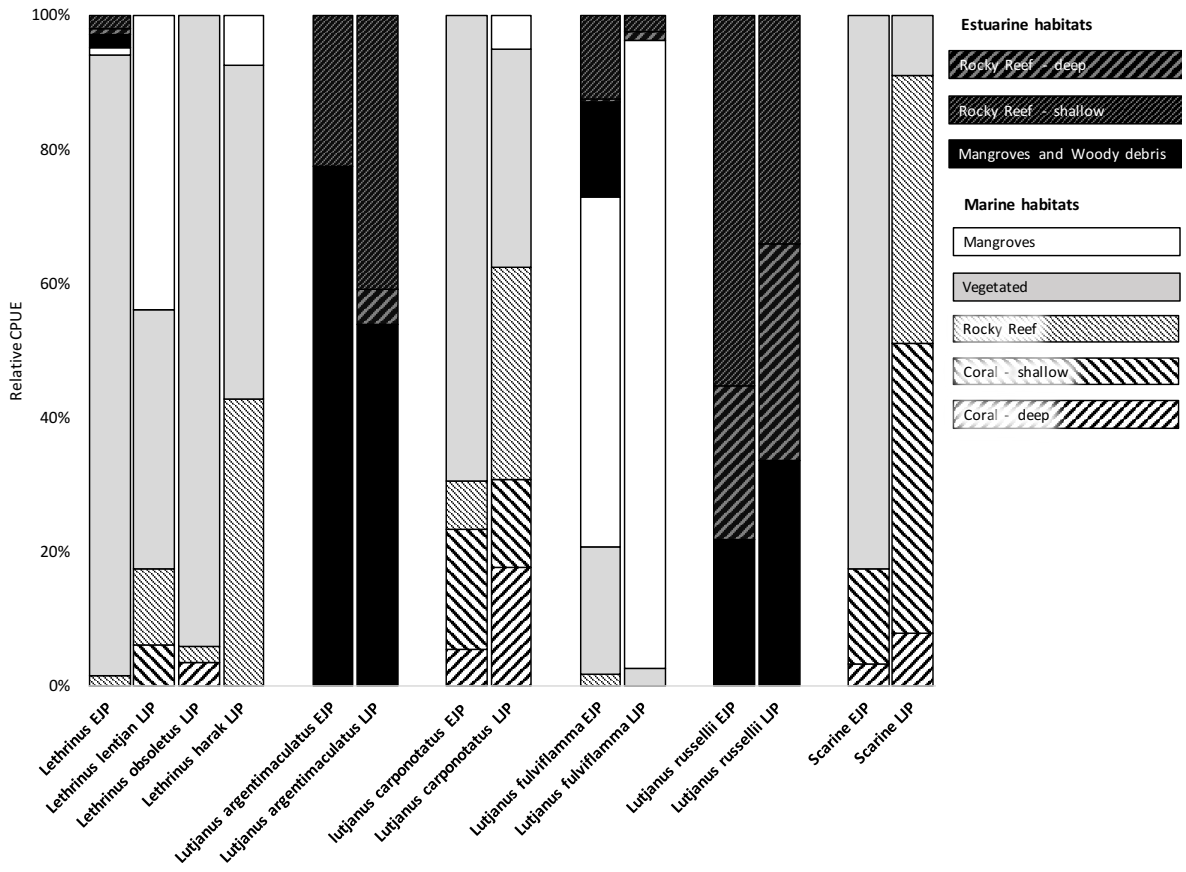


Figure 4.4 Overall habitat use patterns for different juvenile life-stages (*EJP* - Early Juvenile Phase, *LJP* - Late Juvenile Phase) of Lethrinids, Scarines, *Lutjanus carponotatus*, *Lutjanus fulviflamma*, *Lutjanus argentimaculatus*, and *Lutjanus russellii*.

For the Lethrinids, 'Lethrinus EJP' includes all Lethrinus early juveniles - both those individuals that could be identified to species level and those that could not - including but therefore not limited to *Lethrinus atkinsoni, Lethrinus genivittatus, Lethrinus nebulosus, Lethrinus obsoletus, Lethrinus harak*, and *Lethrinus virgatus*. For the Scarines, early juveniles could not be distinguished to species level aside from individuals of the species *Leptoscarus vaigiensis*, and late juveniles could not be distinguished to species level aside from individuals of the species *Scarus rivulatus*

4.4 Discussion

For juvenile fish in my study, the context of a structured habitat – in this case, whether it was in an estuarine or marine area – was more important than the characteristics of that structured habitat – for instance, whether it was a mangrove forest or a rocky reef. Apparently similar habitat types appear to function as a juvenile habitat for a completely different set of species

depending on the marine or estuarine context in which they are found. This provides clear evidence of the over-riding importance of context-dependency in animal-habitat relationships of the coastal zone. Our study demonstrates that habitat types should not be treated as homogenous units, and need to be defined by their environmental context before their habitat functions can be evaluated and predicted.

4.4.1 Mangroves

The *Rhizophora*-dominated mangrove forests of my study area may have a very similar intertidal structural appearance in estuarine and marine waters, but are used by a different set of juvenile fauna. In estuarine environments, mangroves and woody debris appear to function as similar habitat. As far as juvenile fish are concerned, long after a tree has perished, its structural qualities can provide valuable subtidal habitat (Nagelkerken and Faunce 2008). This complex of living and dead trees serve as the predominant juvenile habitat for a range of coastal and reef species. These include important fisheries species such as *Acanthopagrus pacificus*, *A. australis*, *Lutjanus argentimaculatus*, *L. russellii*, *Epinephelus coioides* and *E. malabaricus*. By contrast, sandy mangroves in marine environments appear to function mainly as habitat for juvenile trevally, reef snapper and emperors. While juvenile fish were frequently encountered there, marine mangroves were the predominant juvenile habitat for only two species, *Lutjanus fulviflamma* and *Caranx sexfasciatus*. Marine mangroves on rocky substratums appear to function as an extension of other rocky reef habitat (discussed below). The habitat value of mangroves elsewhere also appears to be defined by estuarine or marine context (Igulu et al. 2014). In Florida, distinct fish assemblages are associated with mangrove prop-root habitat according to estuarine influence, with juvenile lutjanids and haemulids

occurring in near-marine salinity mangroves, and more estuarine taxa predominating upstream (Ley et al. 1999). In the case of the goliath grouper *Epinephelus itajara*, large differences in density, home ranges size and growth were found between estuarine and marine contexts (Koenig et al. 2007), indicating serious fitness differences between contexts. Apparently, context greatly modifies the habitat function of mangroves for juveniles.

4.4.2 Submerged aquatic vegetation

Vegetated soft substratums in marine environments were found to be juvenile habitat for coral reef fish, supporting the most diverse assemblage of juveniles of any habitat surveyed. Importantly, this included both seagrass and macro-algal habitats, which were found in multivariate analysis to be indistinguishable in terms of juvenile assemblage. While seagrass beds are well known juvenile nurseries (Nagelkerken et al. 2000c, Heck et al. 2003), macro-algal beds can also serve a very similar function (Evans et al. 2014, Tano et al. 2017). Very little macroalgae were found in estuarine contexts in my study. Areas of seagrass in estuarine contexts were not commonly used as juvenile habitat. Most juveniles that did use these areas (early juvenile lethrinids, siganids and terapontids) also used marine seagrass and macro-algal beds with much higher rates of encounter. However, a much wider range of terapontid species were found in estuarine seagrass beds, indicating that these beds may serve distinct juvenile habitat functions compared to marine beds. For seagrass beds, their estuarine or marine context appears to determine both the tendency to provide a juvenile habitat function and the species of juveniles that utilise them.

4.4.3 Rocky reef

Rocky reef seems to perform completely different juvenile habitat functions depending on the context in which it is found. In marine environments, it was found to be important juvenile habitat for a range of coral reef fishes, with many of the juvenile species found here also present in shallow coral habitat or marine seagrass. Few species were present at higher densities in rocky reef than these alternative habitats, with the exceptions being late juvenile *Lutjanus carponotatus*, and early juvenile *Scolopsis lineata*. In estuarine environments, rocky reef appears to provide important habitat for snappers, particularly early-juvenile *Lutjanus russellii*, and late-juvenile *Lutjanus argentimaculatus*, *L. johnii* and *L. russellii*. Here, shallow rocky reef harbours a greater diversity of juveniles at a greater density than deep rocky reef, which appears to harbour a depauperate assemblage aside from the wrasse *Halichoeres nigrescens* and late juvenile *L. russellii*. Our results show that rocky reef provides juvenile habitat for different species in estuarine and marine contexts.

4.4.4 Habitat linkages – seascape nurseries

Internal consistencies in juvenile habitat use within estuarine and marine areas suggest that two functionally different 'seascape nursery' types exist at local scales within a region. Our study identified two sets of habitat types inhabited by two sets of juvenile fauna; one defined by estuarine conditions and the other by marine conditions. I found almost no cross-over in the species of juveniles using each seascape type; i.e. each had its own characteristic juvenile assemblage. This indicates that these two seascape types function somewhat independently.

Within each, juveniles of most taxa used more than one habitat type. This finding suggests that individuals are likely to use multiple habitat types within a seascape. Indeed, most nursery species use multiple habitat types (Nagelkerken et al. 2000a, Nagelkerken 2007) to optimise foraging and refuge throughout diel and tidal cycles (Dorenbosch et al. 2004, Hammerschlag et al. 2010). Furthermore, I found evidence that supported the presence of habitat shifts for some species between different juvenile stages (in the species where I could confidently identify different juvenile stages). Shifts in habitat use are common during juvenile development (Kimirei et al. 2011) and appear to be driven by trade-offs between food availability and predation risk (Grol et al. 2014). Together, my results suggest that in both estuarine and marine contexts, juveniles use a mosaic of habitats within seascapes (Sheaves et al. 2015). Seascape nurseries like this have been identified around the world – in the Caribbean, many juveniles settle in coral rubble, move to seagrass beds, then switch to the diurnal occupation of mangroves with nocturnal feeding forays in adjacent seagrass beds (Nagelkerken et al. 2015). However, the presence of distinct types of seascape nurseries operating side by side has not been reported. The presence of multiple nursery seascape types may be common in coastal and nearshore environments globally. In South Africa (Whitfield and Pattrick 2015) and Portugal (Prista et al. 2003), different suites of juvenile fish were found to use estuary systems and adjacent coastal areas. In contrast, in the Middle Atlantic Bight, inner continental shelf habitats function interchangeably with estuarine habitats as nursery grounds for common marine fishes (Woodland et al. 2012). Perhaps only particular coastal settings harbor multiple seascape nurseries, where tidal range, rainfall and geomorphology interact to produce the conditions for segregated juvenile communities. At the very least, we can predict that in low rainfall settings this segregation does not tend to occur (e.g. Nagelkerken et al. 2000a), whereas in high rainfall settings it is at least possible (e.g. this study). I found that multiple kinds of independent seascape nurseries can potentially

operate in close proximity, which has strong implications for local-scale management and conservation of juvenile fish habitats.

4.4.5 Key differences between estuarine and marine seascapes

The differences in juvenile habitat use between estuarine and marine contexts are probably due to a range of factors. A myriad of co-varying contextual factors can be encompassed in the contrast between estuarine and marine areas. The factors that determine nursery function, and the thresholds where this function switches from one type to another, is not definable from this study. Terrestrial runoff simultaneously determines a range of factors that can impact fish distribution, such as salinity (Martino and Able 2003), temperature (Attrill and Power 2004), sediment and nutrient loads (Cyrus 1992, DeMartini et al. 2013), and dissolved oxygen (Eby and Crowder 2002). This is necessarily going to affect how fish use habitats in their aquatic landscape (Marshall and Elliott 1998, Zhang et al. 2009). These factors can in turn define the kinds of biotic habitats present in a location, their spatial configuration, and their micro and macro faunal assemblages (Fabricius et al. 2005), determining food availability and predation risk – elements of context that are intrinsically important in nursery value (Kimirei et al. 2015). This illustrates that habitat value can be a dynamic rather than static property. Changes in rainfall and run-off could alter the assemblages of juveniles using particular habitats in a particular location (Valesini et al. 1997). This means that significant future changes in terrestrial runoff due to anthropogenic drivers such as climate change or upstream development could alter the habitat function of coastal and nearshore habitats (Santos et al. 2018), with important implications for fisheries resource management.

4.4.6 Habitat complexity

For the juveniles identifiable in this study, a pre-requisite for a high probability of encounter in surveys appears to be habitat complexity. Areas with complex structure have long been recognised as important nursery habitat (Beck et al. 2001, Laegdsgaard and Johnson 2001, Heck et al. 2003, Gratwicke and Speight 2005). Structure provides interstitial spaces that can be utilised as refuge by small juvenile fishes (Dahlgren and Eggleston 2000), and the size of interstitial space has been effectively linked to the body size of fish that use it (Hixon and Beets 1989, 1993). Our results corroborate studies that have convincingly demonstrated the relative importance of complex habitat through directly comparable sampling between structured and adjacent unstructured areas (Minello and Rozas 2002) and experimental manipulation (Verweij et al. 2006). However, above a minimum threshold, structural complexity is unlikely to be the only factor that distinguishes valuable juvenile habitat (Grol et al. 2011).

4.4.7 Limitations

I measured probability of encounter and relative abundance (MaxN) in different habitats, both of which indicate frequency or commonality of use, and provide a relative measure of density. Although frequency or abundance of juveniles do not necessarily directly relate to nursery value, in a general sense, high densities of juveniles in a habitat are strongly indicative of nursery function (Prista et al. 2003, Whitfield and Pattrick 2015). As habitat use

is a necessary precondition of nursery function, this is a logical starting point upon which further research can build. While I did not investigate the range of other measures put forward by authors for determining nursery function, such as contribution to adult populations (Beck et al. 2001, Dahlgren et al. 2006), I consider that this was a necessary trade off made in order to take a broad look at the factors structuring juvenile habitat use. It is on this basis that the range of Hinchinbrook region coastal habitats have been discussed above.

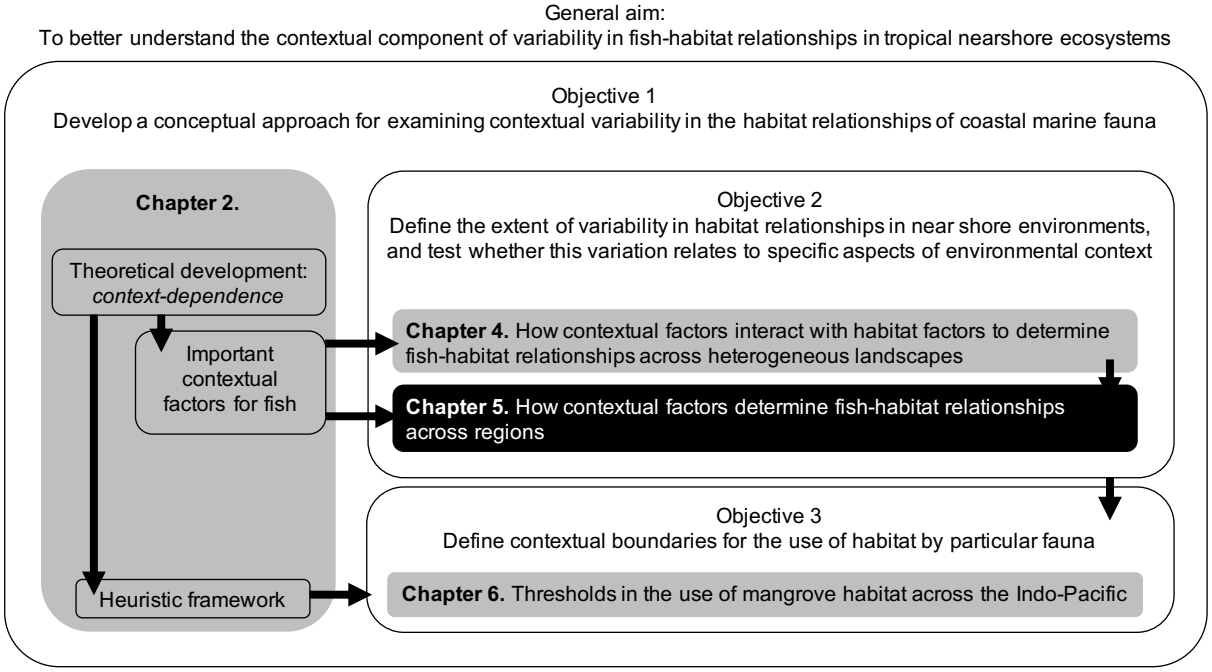
Our study did not account for temporal variation in a strictly orthogonal way due to constraints on optimal sampling conditions and sampling effort. Seasonal peaks in juvenile recruitment, which may either be over or under represented in my dataset, mean that rates of encounter for early juvenile stages are unlikely to be truly representative of the entire year. Therefore, I have focused my interpretation on differences in species composition, rather than absolute rates of encounter, and have included even low encounter habitats in my interpretation of juvenile habitat use (see Appendix A, Table AA2).

4.5 Conclusion

Estuarine and marine areas were used by different juvenile fish, and the habitats found within each area were used in very different ways. Because of this, the habitats occurring in either area should be considered different, even when dominated by the same habitat-forming plants or animals. It is often tacitly assumed that patches of the same habitat type have equivalent ecological roles. These assumptions of equivalence are often employed in ecosystem based species management, the practise of environmental offsetting, and restoration activities.

Wherever they are employed, these assumptions can have serious environmental and social consequences if incorrect. The primacy of context-dependence in the habitat relationships of juvenile fish in my study complicates these assumptions, implying that a robust understanding of context must be considered before equivalence can be assumed with confidence.

5 Local context explains variability in mangrove fish assemblages throughout the Indo-Pacific



5.1 Introduction

Contrasting ideas of habitat function can arise from geographic variation in fauna-habitat relationships. Diverging notions of the importance of different habitat features, and the impact of their removal or modification on species survival and community maintenance, can be the product of large-scale variability in habitat use by fauna (Randin et al. 2006, Zanini et al. 2009). The mechanisms that govern variability in fauna-habitat relationships remain largely undefined. It is generally thought that environmental and ecological mechanisms (e.g. ecophysiological requirements, predation) determine habitat use at smaller spatial scales, and that historic phylogeographic mechanisms (e.g. the available species pool) determine larger scale patterns. However, large-scale patterns must also reflect the outcome of fine scale ecological interactions, driven by differences in environmental conditions (Wiens and Donoghue 2004), such as temperate and rainfall (Whitehead et al. 1992).

There is substantial evidence that variability in fauna-habitat relationships can be partly understood in terms of context-dependence in these relationships (Chapter 2). Physical environmental variation can interact with abiotic constraints of fauna, leading to changes in habitat use that play out over multiple spatial scales. For instance, in terrestrial ecosystems, the use of vegetative structure can depend on climatic gradients, due to the thermoregulatory requirements of fauna. Amphibian and reptile fauna modify their use of tree habitat, shifting from ground-dwelling to arboreal depending on climatic regimes (Adolph 1990, Scheffers et al. 2013). These patterns, observed at regional scales within forests, also explain variation in habitat associations over larger biogeographic scales (Scheffers et al. 2013). Availability of relevant habitat features in the landscape, and constraints on access, will also modify local

habitat use. For instance, in Africa's savanna ecosystems, fauna require access to drinking water, with distance to waterholes a key determinant of habitat use (Redfern et al. 2003, Roever et al. 2012). These access requirements can interact with variation in the physical environment – for example, under wetter conditions, elephants are no longer constrained by distance to waterholes (Roever et al. 2012). Additionally, the use of habitat can be determined by predation risk (Brown 1999), and all of these physical, ecological and landscape factors come together to determine habitat use by African herbivores in the presence of lions (Valeix et al. 2009). In some ecosystems, local environmental forces appear to exert an even greater influence in determining patterns of fauna-habitat association than historical biogeography (Igulu et al. 2014), meaning that some large-scale, global differences in habitat use may be partially explainable in terms of differences in local environmental context.

In this study, I ask whether environmental context can explain the variation observed in habitat use by fishes at both regional and local scales. The association between fish fauna and mangrove habitat provides a useful model system for testing this concept. Mangroves occupy a wide range of environmental settings – from sandy reef flats to freshwater swamps, and are distributed throughout the tropics worldwide (Nagelkerken et al. 2008). Their utilisation by fish is known to vary considerably, both at finer scales (Kimirei et al. 2011), and between regions (Thollot 1992), and as a result, the ecological role of mangrove forests for fish has long been the subject of international debate (Nagelkerken 2009b, Sheaves 2017). This variability complicates our understanding of mangrove-fish relationships, and our ability to employ them, both scientifically (Faunce and Layman 2009) and in conservation and environmental management (Sanchirico and Mumby 2009).

The physical environment, landscape scale habitat requirements, and constraints on access, all strongly influence the use of coastal habitat by fish in general, and appear particularly important in determining the use of mangroves. Firstly, salinity can structure fish assemblages throughout the coastal zone due to differing salinity tolerances (Harrison and Whitfield 2006, Whitfield et al. 2006). Salinity can determine the fish assemblages found in mangroves at regional scales (Ley et al. 1999), and appears to be a major determinant of mangrove habitat function globally (Igulu et al. 2014). Secondly, the surrounding seascape can have a profound influence on how fish use coastal habitats, with connectivity or distance between mangroves and reefs of particular importance (Nagelkerken et al. 2012, Olds et al. 2012a) due to the ontogenetic use of mangroves by reef fish (Dorenbosch et al. 2007, Pittman et al. 2007, Jones et al. 2010). Finally, the tidal amplitude experienced in a region can profoundly shape how intertidal habitats like mangroves are used by fish (Sheaves 2005). In areas with small tidal amplitudes, fish are able to use mangrove habitat continuously (Dorenbosch et al. 2007), whereas in areas of large tidal amplitudes, mangroves are exposed at low tide, and the duration of exposure can vary substantially among regions (Baker et al. 2015). To utilise these intertidal habitats, fish are forced to perform potentially risky intertidal migrations (Dorenbosch et al. 2004, Unsworth et al. 2007). The magnitude of inundation can shape the use of intertidal habitat within regions (Rozas 1995, Minello et al. 2012), and is thought to be a primary driver of the use of mangroves by juvenile fishes globally (Igulu et al. 2014). While each of these three drivers have received considerable attention individually, it has been difficult to study how their interplay shapes fish assemblages. This is because field studies have tended to standardise variation in one or more of these variables through site selection, and because the array of different sampling techniques used in different locations precludes a robust understanding across different environmental contexts.

Can environmental factors such as these predict fauna-habitat associations over multiple spatial scales? Until now, there has been no evaluation of how their combined influence determines patterns in species habitat associations across regions using directly comparable data. Therefore, the aim of this study is to understand the role of environmental context in defining habitat associations. Specifically, I aim to examine the breadth of variation in mangrove fauna that occurs naturally within and between regions in the Indo-Pacific. While there are differences in species distributions across this realm driven by biogeographic forces, at the family level, most taxa are present throughout the realm, due to a shared evolutionary history (Cowman and Bellwood 2013). By examining patterns in family level use of mangrove forests, I aim to examine broad differences that cannot be attributed solely to biogeography. I aim to compare the extent to which the use of mangroves differs within and between regions, and how much of this variation can be attributed to environmental conditions. At the scale of the Indo-Pacific, environmental conditions are not distributed evenly between regions, due to differences in climate, geomorphology and tidal regimes, therefore any response to local environmental factors will also manifest as differences between regions to some extent. The important question is whether the response of fauna is consistent with the distribution of environmental variation. In essence, can we predict mangrove habitat use based on environmental proxies, irrespective of biogeographical processes and patterns?

5.2 Methods

5.2.1 Study sites:

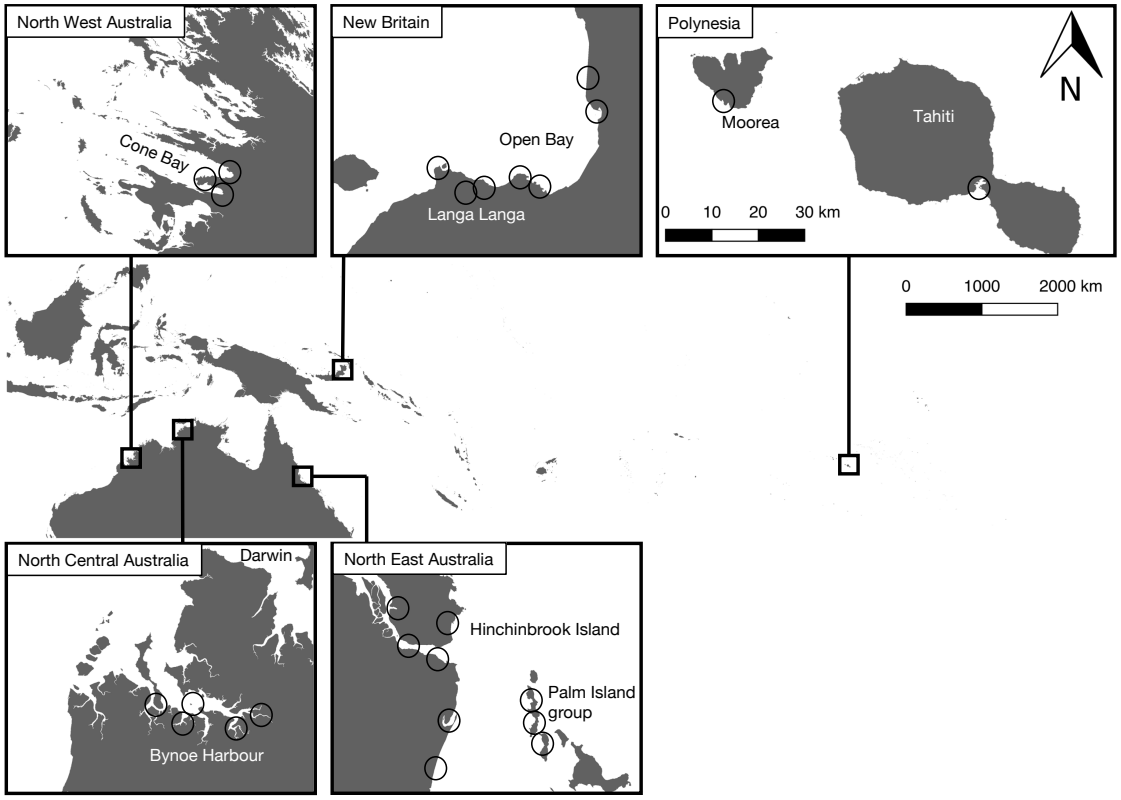


Figure 5.1 Distribution of sampling effort.

Central map shows the eastern Indo-Pacific, and the location of my study regions. Each study region map is identically scaled (scale bar located in French Polynesia map). Black circles show video sampling sites.

Study sites (Figure 5.1) were selected to examine mangrove fish fauna across an approximation of the contextual range of mangrove habitat in the Indo-pacific (see Table 5.1). These locations cover almost the entire spread of tidal amplitudes in the Indo-Pacific, from 0.5m to 11m. Within each location, efforts were made to cover the full range of

variation present in distance to reef, and salinity. Some locations have larger variation in distance to reef than others due to the underlying geomorphological composition of the seascape. Similarly, some locations have larger variation in salinity than others, due to differences in rainfall. These imbalances in the dataset are representative of natural variation, and do not violate any underlying assumptions in the exploratory analyses that I employed. All results were interpreted with these imbalances in mind.

Table 5.1 Regional sampling details, including environmental parameters and associated meta-data.

Climate data from www.climate-data.org, accessed October 2018. Tidal pattern data from data.shom.fr, accessed October 2018.

Region	**Tidal range**	**Tidal pattern**	**Sampling period**	**Climate, yearly average rainfall.**	**Salinity: range sampled**	**Distance to reef: range sampled**	**Coordinates**
Polynesia	0.5m	Semi-diurnal with diurnal inequality	October 2017	Tropical monsoon climate, 1800mm	32-34ppt	30m-360m	17° S 149° W
New Britain	0.9m	Mixed	September – November 2015 & 2016	Tropical monsoon climate, 3700mm	0-35ppt	30m-14km	4° S 151° E
North eastern Aust.	3.9m	Semi-diurnal with diurnal inequality	June – December 2014 & 2015	Tropical monsoon climate, 2237mm	0-35ppt	30m-25km	18° S 146° E
North central Aust.	7.8m	Semi-diurnal with diurnal inequality	September 2015	Tropical savanna climate ,1694mm	29-35ppt	1km-27km	12° S 130° E
North western Aust.	10.8m	Semi-diurnal	June 2017	Tropical semi-arid climate, 562mm	34-35ppt	30m-8km	16° S 123° E

5.2.2 Fish Surveys

I sampled fish assemblages using remote unbaited video census. Video surveys were conducted throughout the day and tidal cycle, in an attempt to adequately represent natural variability. Cameras were deployed inside mangrove habitat structure, within the first 2 metres of the seaward edge of the mangrove forest. Videos were deployed and processed as per the methods described in Chapter 3. This produced 389 video samples for analysis. Only presence/absence data was used in the following analysis, as both schooling and solitary species could be encompassed within family groups, making abundance data non-comparable between locations. Some taxa could not be identified to level of family, including Gobiiform and Clupeiform fishes, and these are instead recorded at the level of order in the data presented below.

5.2.3 Explanatory variables:

5.2.3.1 Salinity

Salinity surveys were carried out at each location during each sampling trip using either a refractometer or salinometer, measured in parts per thousand. These surveys were conducted concurrently with video sampling, but measurements were not taken for each video recording individually. Therefore, salinity values represent the shallow water readings associated with the area, rather than individual position and time of each video sample. As sampling was carried out outside the monsoon season for each location, I am making the assumption, based

on previous research carried out in these locations (Wolanski et al. 1990, Aharon 1991, Wolanski and Spagnol 2003, Langer and Lipps 2006, Williams et al. 2006, Baker et al. 2018) that waters were reasonably well mixed and salinity was not fluctuating dramatically during the sampling period, making these values adequately representative.

5.2.3.2 Distance to reef

Distance to reef was measured using the shortest path through water between the sample, as recorded by GPS position, and the nearest visibly identifiable patch of biogenic (coral) reef from satellite imagery. A variety of satellite sources were used to avoid cloud cover and view areas under low wind and low tide conditions to maximise the possibility of reef detection, including Google earth, ARC GIS and DigitalGlobe (http://www.digitalglobe.com/, accessed August 2018). Ground sample distance (i.e. resolution) ranged between 65cm and 39cm. While this method may miss minor patches and deeper reefs, it provides a good indication of the distance from a point to the nearest substantial photic-zone reef.

5.2.3.3 Regional tidal amplitude

The maximum tidal amplitude of the region in which the video sample was taken was used as an explanatory variable. Values were derived from tidal gauge data, obtained from Australia's National Tidal Centre and University of Hawaii's Sea Level Centre (Caldwell et al. 2015).

5.2.4 Data analysis:

Family level taxonomic assemblage composition was quantified for each sample. While there are differences in the species pool in the different regions sampled, all broadly contain the same families of near-shore fishes (Sheaves 2012). Therefore, I am using family level taxonomic assemblage to obtain a comparable metric by which to assess differences in the use of mangrove forests by fish throughout my study sites. Fishes from the families Gobiidae and Blenniidae could not be reliably distinguished in video samples, therefore the order Gobiiformes was used. Similarly, fishes from the families Atherinidae, Clupeidae and Engraulidae could not be reliably distinguished, and the order Clupeiformes was used. The distinction between Scarinae and other labrid fishes was maintained due to their broadly divergent functional ecologies.

5.2.4.1 Multidimensional scaling

Multivariate data that is dominated by absences can present problems during analysis due to the undue influence of rare taxa and empty samples (Clarke et al. 2006). Therefore, rare taxa are often excluded from multivariate analyses. However, taxa that are rare at the level of the entire dataset can still be important, as they might be common in one region and absent in others. To account for this, taxonomic assemblage data were treated in two different ways, to examine whether any observed patterns were robust. In the first, more conventional treatment, an arbitrary dataset wide cut-off was used to determine the inclusion of taxa in

analysis (e.g. Davis et al. 2014). All taxa present in less than 10% of total samples were excluded, which removed all taxa with low occurrences regardless of regional occurrence rates, providing a dataset with minimal influence of rare taxa. In the second, more inclusive treatment, taxa present in at least 10% of samples from any one region were retained in the analyses. This only removed taxa that were rare throughout all regions, and provided a dataset where all non-trivial differences between regions would be maintained. This treatment resulted in substantial outliers in subsequent analysis. These outliers were excluded from the dataset, providing a third and final data treatment. To examine the variation in taxonomic community composition in all treatments, Jaccard's coefficient similarity matrices were calculated on the binary presence or absence of each taxonomic group in each sample. Non-metric multidimensional scaling (MDS) applied to these similarity matrices was used to display patterns of multivariate variation graphically, to examine the taxa that characterised this variation and relationships in their co-occurrence. This was performed using the 'metaMDS' function in package Vegan (Oksanen et al. 2013) in R. The conventional treatment produced a two-dimensional MDS solution with an acceptable (<0.2) level of stress (see Appendix B, Figure AB1). The inclusive treatments resulted in high stress two-dimensional MDS solutions (see Appendix B, Figure AB2 and AB3), therefore lower stress three-dimensional solutions were produced, and the first two dimensions (which capture the bulk of variation in the data) were examined. Due to general agreement between the different data treatments, only the results of the inclusive treatment excluding outliers is presented in the main text. The results of the other two treatments are provided in the Appendix (Appendix B, Figures AB4 to AB7).

5.2.4.2 Multivariate Regression Tree Analysis

To examine whether the broad variation in taxonomic community composition could be explained by environmental context, a multivariate regression tree analysis was performed with the mvpart package in R (De'ath 2007, Ouellette and Legendre 2012). This technique recursively partitions the dataset into homogenous subgroups using explanatory variables, in this case the three descriptors of environmental context; salinity, distance to reef and tidal amplitude. For each partition, the machine learning analysis considers all three explanatory variables, and selects the variable that maximises the decrease in group heterogeneity. In the final tree, the variables that were selected, and how the dataset was partitioned, allowed me to understand how these variables explain community structure when considered together. The importance of each contextual variable in explaining variability in the tree model was also calculated based on the reduction in mean squared error by each candidate variable at each split, using the caret package in R (Kuhn 2012). Regression tree approaches are robust to the suspected co-variation in explanatory variables as described above (Table 5.1). The tree examined was based on the inclusive data treatment excluding outliers, as described above, in order to preserve regional differences and exclude the undue influence of outliers. The analysis was based on the same multivariate taxonomic similarity matrix used in the MDS analysis above.

5.2.4.3 Surface fitting

To examine how each environmental contextual variable related to the variation in taxonomic community composition observed, surface fitting of explanatory variables was applied to the

MDS ordinations. This technique uses generalized additive models to fit a smooth surface, with the degree of smoothing determined by generalised cross validation, and was carried out using the 'ordisurf' function in package Vegan (Oksanen et al. 2013) in R. This technique is appropriate for examining relationships between environmental variables and community composition when relationships are not necessarily linear, as is assumed in vector fitting.

5.3 Results

In total, 45 different higher level fish taxa were found in mangrove habitats throughout this study. Most taxa were only present in mangroves in certain regions, with the exception of Carangidae, Gobiiformes and Lutjanidae, which were present in mangroves throughout the Indo-Pacific (Table 5.2). Few of these families were commonly encountered, with only 9 families occurring in greater than 10% of total samples.

Table 5.2. Proportional presence in video samples of different fish taxa by region

Values show the percentage of videos in which a taxon was present. Regions are ordered by increasing tidal amplitude, and the total number of samples analysed for each region is presented in the first row (total n). Taxon retained for analysis in the conventional data treatment are identified with an asterisk (*), and taxon retained for analysis in the inclusive data treatment are identified in bold.

	Polynesia	New Britain	NE Aust.	NC Aust.	NW Aust.
Total n	55	98	157	28	51
Acanthuridae	27.3	1.0	1.9	0.0	2.0
Ambassidae*	0.0	20.4	12.1	0.0	11.8
Apogonidae*	3.6	36.7	2.5	0.0	0.0
Ariidae	0.0	0.0	0.0	21.4	5.9
Balistidae	7.3	0.0	0.0	0.0	0.0
Belonidae	0.0	1.0	0.0	0.0	0.0
Carangidae	10.9	7.1	9.6	3.6	15.7
Carcharhinidae	3.6	0.0	3.2	0.0	0.0

Chaetodontidae	38.2	4.1	5.1	0.0	0.0
Clupeiform	0.0	0.0	7.0	3.6	3.9
Dasyatidae	0.0	0.0	1.3	3.6	2.0
Diodontidae	1.8	0.0	0.0	0.0	0.0
Drepaneidae	0.0	0.0	0.6	3.6	7.8
Eleotridae	0.0	2.0	0.0	0.0	0.0
Gerreidae*	0.0	6.1	48.4	7.1	15.7
Gobiiform*	7.3	19.4	37.6	25.0	37.3
Haemulidae	0.0	5.1	3.2	3.6	5.9
Hemiramphidae	0.0	2.0	0.0	0.0	0.0
Holocentridae	7.3	0.0	0.0	0.0	0.0
Labridae	14.5	3.1	10.2	3.6	0.0
Latidae	0.0	0.0	3.2	3.6	2.0
Leiognathidae	0.0	6.1	4.5	7.1	9.8
Lethrinidae	0.0	0.0	20.4	0.0	0.0
Lutjanidae*	74.5	87.8	55.4	14.3	29.4
Monodactylidae	0.0	8.2	5.7	0.0	2.0
Mugilidae	23.6	7.1	6.4	0.0	17.6
Mullidae*	60.0	6.1	4.5	0.0	0.0
Nemipteridae	0.0	14.3	0.6	0.0	0.0
Ostraciidae	12.7	0.0	0.0	3.6	0.0
Pomacanthidae	0.0	0.0	0.6	0.0	0.0
Polynemidae	1.8	0.0	0.0	0.0	0.0
Pomacentridae*	56.4	26.5	8.9	0.0	0.0
Pseudomugilidae	0.0	0.0	5.1	0.0	0.0
Scarinae	29.1	0.0	7.6	0.0	0.0
Scatophagidae	0.0	7.1	3.2	10.7	7.8
Serranidae	0.0	16.3	1.3	0.0	9.8
Siganidae*	5.5	9.2	19.1	0.0	2.0
Sillaginidae	0.0	0.0	1.9	0.0	9.8
Sparidae*	0.0	3.1	47.1	21.4	51.0
Sphyraenidae	0.0	1.0	5.7	0.0	3.9
Terapontidae	0.0	4.1	0.6	0.0	11.8
Tetraodontidae	12.7	2.0	3.8	0.0	7.8
Toxotidae	0.0	17.3	8.9	0.0	0.0
Zanclidae	18.2	0.0	0.0	0.0	0.0

5.3.1 Variation in mangrove fish assemblages

Overall, multidimensional scaling revealed that there was substantial variation in family level taxonomic composition of video samples both within and between regions. Due to overall agreement between different data treatments, only the final treatment (inclusive of taxa that were common within regions, but excluding outliers) is presented in detail (Figure 5.2). Samples from French Polynesia and Papua New Guinea, characterised by Scarinae, Labridae, Acanthuridae, Chaetodontidae, Pomacentridae, Ostraciidae, Zancillidae, Mullidae, Nemipteridae and Apogonidae, were separated from the majority of samples from Northern Australian regions, which were characterised by Gobiiformes, Gerreidae and Sparidae. Differences between regions appear to be an important contributor to the overall variation of mangrove fish assemblages across the Indo-Pacific. There was also clear overlap of the regions within these two regional clusters, and some overlap of these two regional clusters (Figure 5.2). This indicates that a substantial portion of the variation in fish assemblages is not explainable in terms of regional difference, and occurs within each region individually. Many samples were more similar to samples in other regions than to the majority of the samples from their own region, demonstrating that mangrove assemblages can be quite similar between regions. The magnitude of variation between samples captured primarily on dimension 1, which appears to capture differences between regions, is similar to the magnitude of variation that is captured on dimension 2, which appears to capture differences between samples within regions. North Eastern Australia had the widest spread of all regions, covering the entire ordination space. This demonstrates that mangrove assemblages can be highly variable within a region, and implies that this variation can in some cases equal the entire span of variation among regions. Both the conventional data treatment (see Appendix

B, Figure AB4) and the inclusive treatment prior to removal of outliers (see Appendix B, Figure AB5) captured these same general patterns within and between regions.

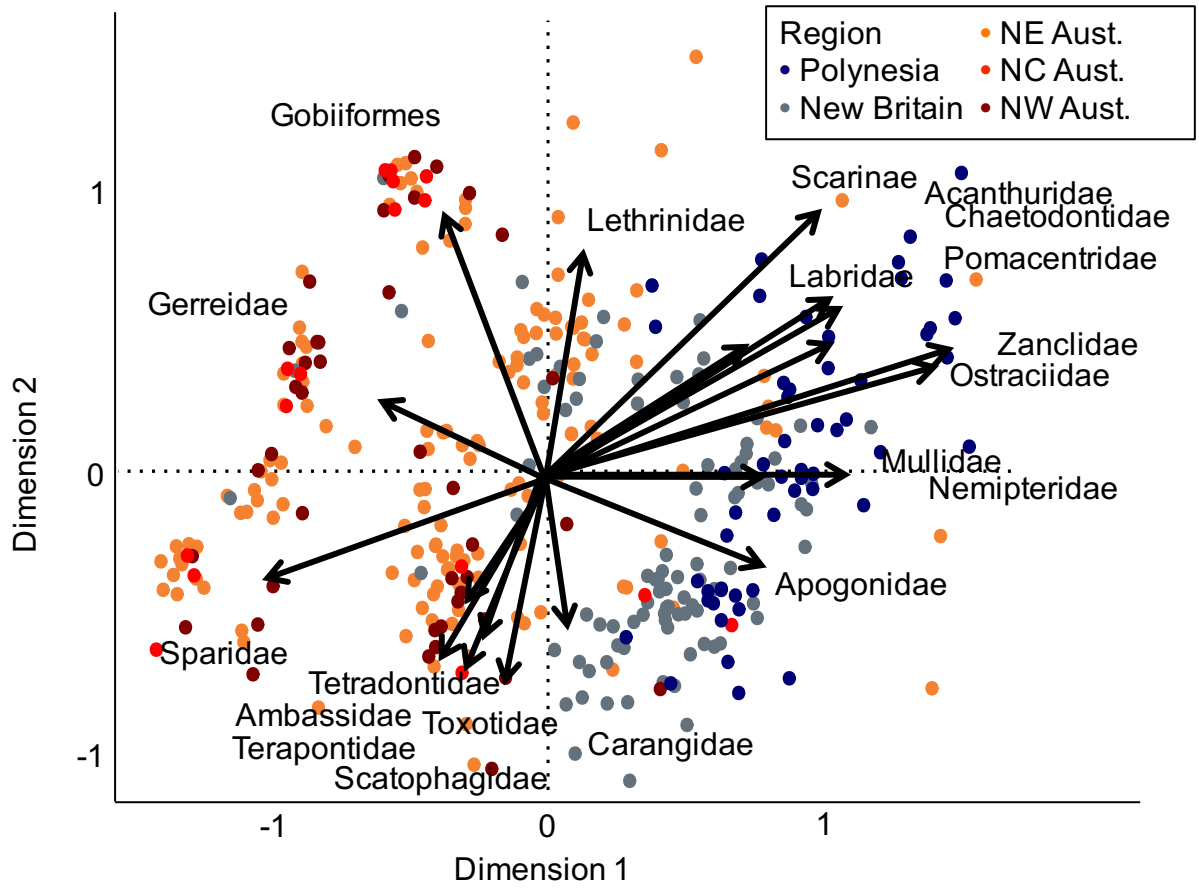


Figure 5.2 MDS ordination displaying the first two dimensions of a 3D solution (stress: 0.152) capturing the differences between samples based on an inclusive data treatment (excluding outliers) of family level taxonomic assemblage composition (n=349).

Dimensional values are scaled such that a distance of one unit represents a halving of assemblage similarity between samples. Taxonomic vectors represent the direction of positive correlation with the ordination space. Vector terminal position represents a taxa's centre of occurrence in the ordination space, calculated using the weighted average of sample abundances. Only taxa that are far (>0.5 dimensional units) from the centre of the ordination space (i.e. taxa that differ strongly across the ordination space) are shown. Points have been jittered (at a scale of 0.1 on each dimensional axis) to reveal quantities of points occurring at identical positions in the ordination.

5.3.2 Potential contextual drivers of variation in mangrove fish assemblages

All three potential contextual drivers were selected by multivariate regression tree analysis as factors that were useful in explaining the structure of variability within the dataset. The resulting tree structure (Figure 5.3) indicates the primacy of tidal amplitude in defining mangrove assemblages. The major division in the dataset was between small (<2.16m) and large (>2.16m) tidal amplitudes. Within samples from small tidal regimes, variability was best explained by the tide again, effectively distinguishing between samples from Polynesia (0.5m tidal range) and New Britain (0.9m tidal range). Within samples from large tidal amplitudes, the biggest difference between community composition was between sites close to reefs (<560m) and sites far from reefs (>560m). Samples from large tidal amplitudes close to reefs varied most according to tidal amplitude again. Samples from large tidal amplitudes far from reefs were diverged most according to salinity, with samples in salinities below 28ppt (i.e. brackish waters) distinct from those in salinities above 28ppt (i.e. near-marine and marine waters). Variable importance values (Table 5.3), indicated that tidal amplitude was the most important factor in explaining variability in the dataset. Salinity and distance to reef had very similar importance values, meaning that they were both equally capable of partitioning variation. Together, these results demonstrate that tidal amplitude can explain much of the variation in community composition throughout the Indo-Pacific, and highlights that while distance to reef and salinity are also important, their effects are highly interactive with tidal range.

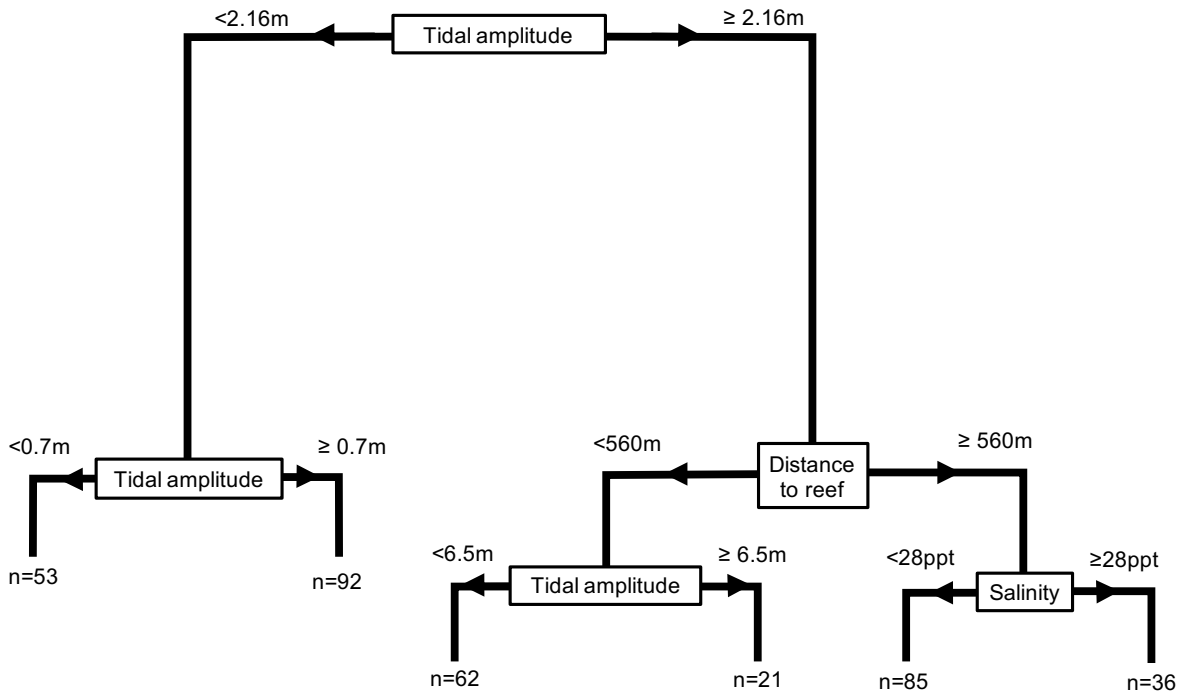


Figure 5.3 Multivariate regression tree describing the major divisions in community composition of mangrove habitat based on environmental context, throughout the Indo-Pacific (n=349).

Each division is labelled by the contextual factor that is best able to split the data into homogenous groups, and the values that best distinguish them. The difference between group community structure is proportional to vertical distance in the dendrogram.

Table 5.3 Variable importance for the three contextual variables used in multivariate regression tree analysis.

Predictor	Rank	Reduction in MSE	Proportional reduction in MSE relative to best predictor
Tidal amplitude	1	0.56	1
Salinity	2	0.37	0.66
Distance to reef	3	0.35	0.63

Surface fitting was used to model the gradient of change for each of the three explanatory context variables across the ordination space (Figures 5.4, 5.5 and 5.6). Salinity, distance to reef and tidal amplitude were all significantly correlated with the ordination ($p<0.001$),

meaning that the distribution of points was in some way concordant with changes in values of each of these variables. The variation explained by each variable differed markedly. The amount of variation in the ordination explained by each model indicates how closely changes in assemblage composition across the space mirror changes in the values of each variable. By examining surface plots, we are able to see how modelled gradients in each variable relate to fish families and regional groupings. Findings were consistent across all three different data treatments for the exclusion of rare taxa (see Appendix B Figures AB6 and AB7).

Salinity explained 14% of the variation in the ordination space, meaning that while there was not extensive agreement between salinity values and assemblage composition, there was still a meaningful pattern across the space (Figure 5.4). Variation across much of the space is likely driven by tidal range and distance to reef, as indicated by the multivariate regression tree (Figure 5.3), where salinity was the most important discriminator only within particular tidal amplitudes and distances from reef. Salinity appears to predominantly describe variation that occurs within regions rather than between them (Figure 5.4a), with the gradient mainly occurring along dimension 2. Sparidae, Gerreidae, Tetraodontidae, Ambassidae, Toxotidae, Carangidae, Terapontidae and Scatophagidae appear to be associated with brackish salinities, and Gobiformes, Lethrinidae, Scarinae, Labridae, Acanthuridae, Chaetodontidae, Pomacentridae, Ostraciidae, Zancillidae, Mullidae and Nemipteridae associated with higher salinities (Figure 5.4b).

Distance to reef explained 46% of the variation in the ordination, indicating that there was a strong agreement between this variable and assemblage composition (Figure 5.5). The surface appears to explain variation both within and between regions, with the gradient

running diagonally across the space, varying substantially over both dimensions 1 and 2 (Figure 5.5a). Gobiformes, Sparidae, Gerreidae, Tetraodontidae, Ambassidae, Toxotidae, Carangidae, Terapontidae and Scatophagidae appear to be associated with large distances from reefs, and Scarinae, Labridae, Acanthuridae, Chaetodontidae, Pomacentridae, Ostraciidae, Zancillidae, appear to be associated with small distances from reefs (Figure 5.5b).

Tidal amplitude explained 61% of the variation in the ordination, indicating that there was a very strong agreement between this variable and assemblage composition (Figure 5.6). The gradient in tidal amplitude is generally linearly correlated with dimension 1, mirroring the broad differences in regions captured across the ordination space (Figure 5.6a). The strong gradient apparent on the surface plot between micro-tidal (Polynesia and New Britain) and macro-tidal regimes (Northern Australia), indicates that tidal amplitude explains differences in this part of the space, but the lack of a gradient over Northern Australian samples indicates that other factors are important in this part of the space. This is consistent with the multivariate tree (Figure 5.3). Scarinae, Labridae, Acanthuridae, Chaetodontidae, Pomacentridae, Ostraciidae, Zancillidae, Mullidae, Nemipteridae and Apogonidae appear to be associated with small tidal amplitudes and Gobiiformes, Gerreidae and Sparidae appear to be associated with large tidal amplitudes (Figure 5.6b).

Each variable appears to explain a somewhat different component of variation in the ordination space. Gradients occurred along different axes, reflecting the separation between different sets of species. However, both distance to reef and tidal range explained variation

occurring along dimension 1, indicating that they co-varied across my study regions. As a result, these three variables explain more than 100% of the variation in the ordination space, i.e. variation is not strictly partitioned between them.

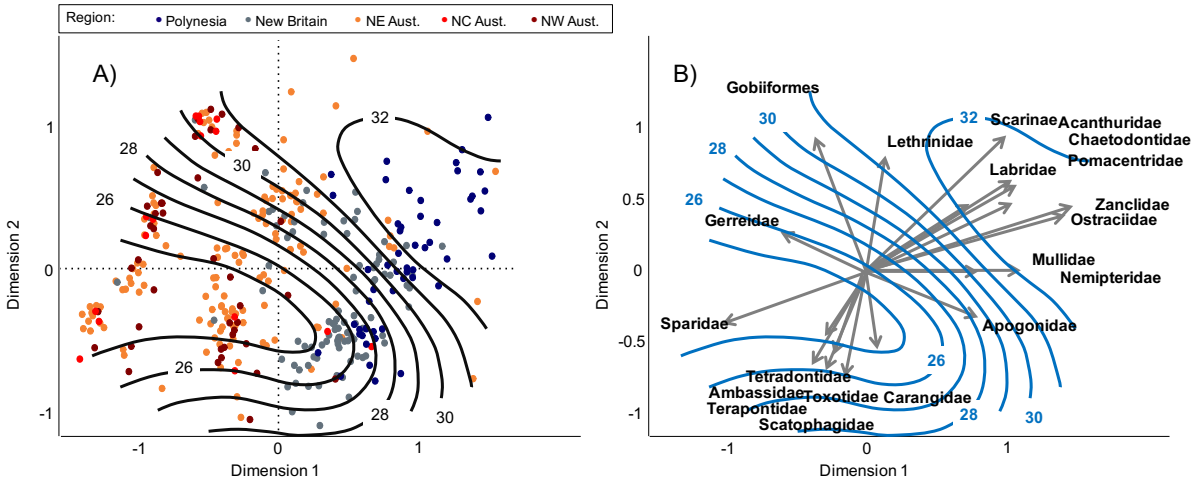


Figure 5.4 Surface fitting of salinity as an explanatory variable.

Panel A shows surface with sample points for reference, Panel B shows surface with species vectors for reference. Lines describe the topography of the gradient, and units are in parts-per-thousand. Deviance explained: 14.5%

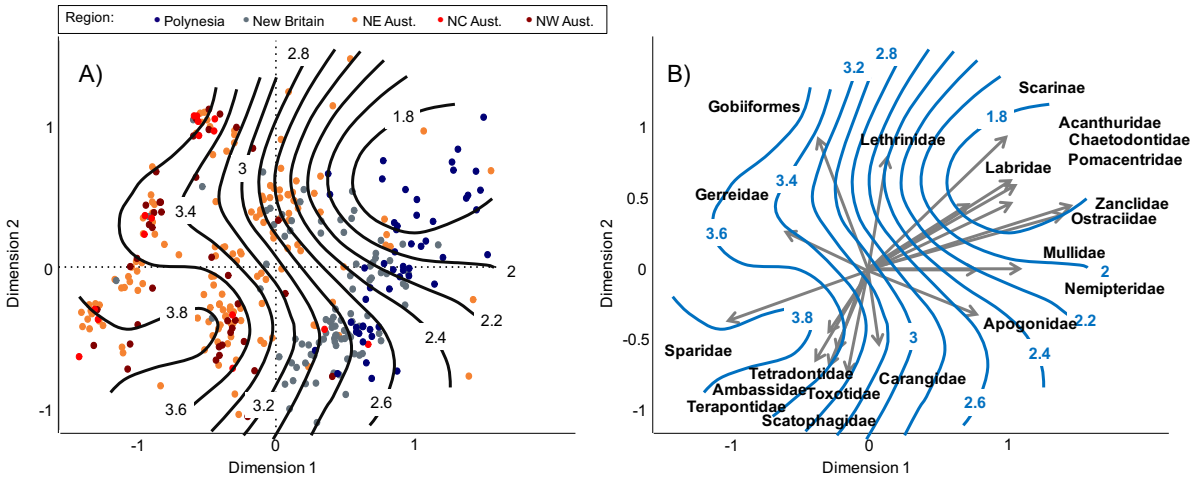


Figure 5.5 Surface fitting of distance to reef as an explanatory variable.

Panel A shows surface with sample points for reference, Panel B shows surface with species vectors for reference. Lines describe the topography of the gradient, and units are in log (metres). Deviance explained: 46.4%

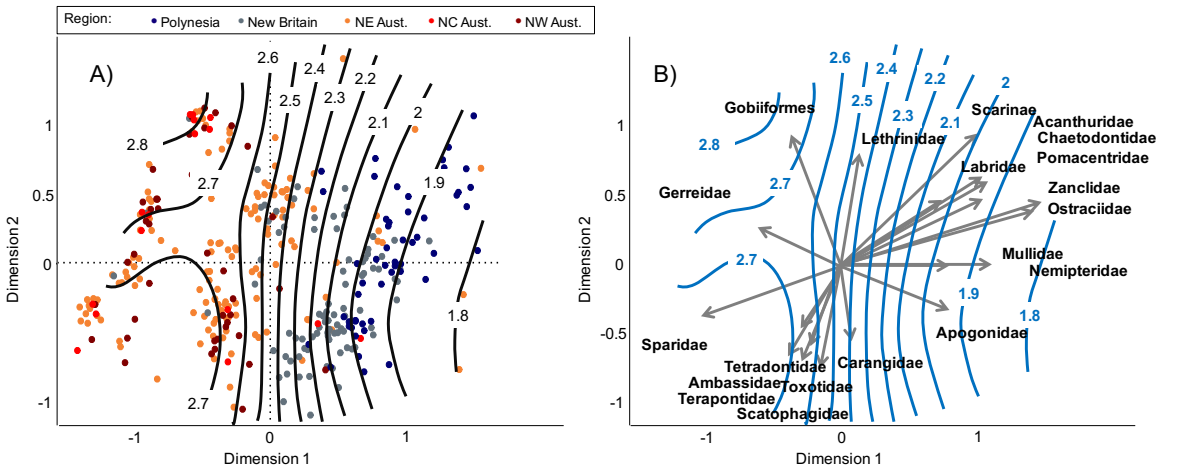


Figure 5.6 Surface fitting of Tidal amplitude as an explanatory variable.

Panel A shows surface with sample points for reference, Panel B shows surface with species vectors for reference. Lines describe the topography of the gradient, and units are log (cm). Deviance explained: 60.9%

5.4 Discussion

Environmental context appears to explain variation in the habitat associations of fishes at both regional and local scales across the Indo-Pacific. Faunal composition was clearly not region specific. Regions showed considerable overlap in assemblage composition, with the spread of North Eastern Australia samples covering almost the entire spread of variation seen between regions. Instead, the response of fish fauna was largely consistent with environmental variation. Regions with broadly similar tidal amplitudes showed considerable overlap in assemblage composition. Tidal amplitude has been identified as a potential global determinant of the use of mangroves by fish (Faunce and Layman 2009, Igulu et al. 2014), and results from my study supports this hypothesis. The variation within broadly similar tidal regimes was explained by both salinity gradients and seascape structure. This is consistent with the findings of other mangrove studies from across the Indo-Pacific, which together show that geographically distant mangrove forests in similar environments can share similarities in fish taxa. In marine environments close to reefs, mangroves tend to be characterised by taxa such as Pomacentridae and Apogonidae (Unsworth et al. 2009, Barnes et al. 2012). In brackish environments far from reefs, mangroves tend to be characterised by coastal and estuarine taxa such as Ambassidae and Sparidae (Blaber et al. 1989, Sheaves et al. 2016). This is not the only important axis of variation in these two factors. In large tidal amplitude regions, in mangroves far from reefs, there was an important difference in fish fauna based on salinity alone. This is consistent with the idea that salinity plays a key role in structuring fish fauna in coastal and estuarine environments (Weinstein et al. 1980, Ley et al. 1999). These results are consistent with the idea that variation in habitat use is driven by environmental conditions, and demonstrate that in the Indo-Pacific, context can explain differences in the use of coastal habitats by fauna.

The commonalities in mangrove assemblages found in similar contexts appear to be independent of historical biogeography. Tidal amplitude was useful in partitioning the major differences in assemblages from across the Indo-Pacific, and consistently explained more than half of the variation observed in mangrove assemblage composition. However, in this study, differences in the extremes of tidal range also represented extremes in distance to reef. The amphidrome point of the South Pacific lies far from any major landmasses (Luther and Wunsch 1975), meaning that areas with the smallest tidal regimes lack extensive areas of mangroves far from reefs. Samples from Polynesia were all less than 500m from reefs, whereas a large proportion of samples from North Central and North West Australia were greater than 500m from reefs, so the extremes of both variables are confounded in this analysis, which explains why these variables together explain >100% of the variation observed in the ordination. In addition, large differences in tidal regime will always be inextricably confounded with biogeography in some ways, as large differences in tidal regime tend to occur over large geographic scales (Luther and Wunsch 1975). While the use of family level taxonomic composition avoids much of the differences between regions caused by species ranges (Sheaves 2012), some of the families that distinguished North Central and North Western Australian samples are entirely absent from French Polynesia – namely Sparidae and Gerreidae (Froese and Pauly 2018), so their absence from mangroves there can be attributed directly to biogeography. However, these families are common in New Britain, and their absence from mangroves there still serves to distinguish samples in this region from those with larger tidal ranges. Similarly, these families are common in North Eastern Australia (Froese and Pauly 2018), and their presence or absence appears to distinguish between mangroves close to and far from reefs. Importantly, none of the families that distinguished Polynesia and New Britain were unique to these regions – they are all common

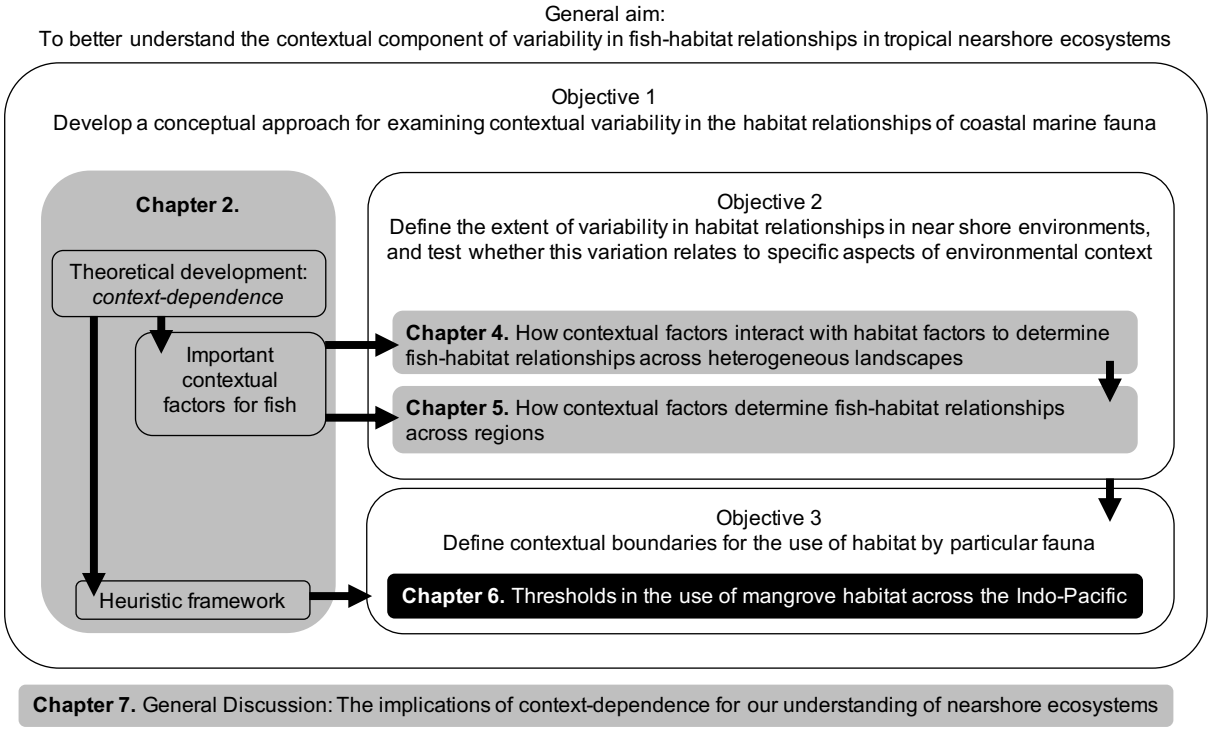
taxa found in all regions sampled, yet they were absent from mangroves in all northern Australian regions. Between the extremes of tidal amplitude, differences in assemblages are inextricably confounded among contextual factors and biogeography. However, assemblages from intermediate tidal amplitudes that contained a full spread of variation in salinity and distance to reef (New Britain and North Eastern Australia), consistently resembled assemblages from extreme locations that were most similar in terms of environmental context. This demonstrates that there are strong commonalities in mangrove assemblages found in low tidal amplitudes close to reefs, and in high tidal amplitudes far from reefs, that are independent of historical biogeography.

The way in which these multiple factors might interactively determine the use of coastal habitats by fish is not well understood. It is possible that the direct ecological costs of inhabiting mangroves in regions where they are routinely exposed during the tidal cycle shapes fish assemblages. Regular migration between mangroves and suitable low tide habitat are likely to involve increased opportunities for predation (Gilliam and Fraser 2001), and incur a substantial energetic cost (Bernatchez and Dodson 1987, Alexander 2002). In these regions, the duration, frequency and depth of inundation of intertidal habitats all vary with tidal amplitude (Minello et al. 2012, Baker et al. 2015), and fish that use mangroves would need to respond to these dynamics with strategies for coping with temporal variation in connectivity, including inter-habitat migrations (Sheaves 2005). In tidally influenced areas, mangroves might be predominantly inhabited by taxa that have developed adaptations to these challenges. Under these conditions, the surrounding seascape, particularly the kind of habitat that is available at low tide, will strongly influence the set of fish that are able to use mangrove habitat (Sheaves 2005). Some of the variation observed in this study could relate to

qualities of the surrounding seascape that were not examined, such as distance to subtidal habitats other than reef, e.g. seagrass (Gilby et al. 2016). As the results of this study suggest, tidal amplitude and seascape structure are likely to interact to determine the use of intertidal habitat by fish. Overall, regional differences in the Indo-Pacific are likely due to the pervasive, ecosystem wide effects of differences in climate, geomorphology and tidal regime.

While there is certainly taxonomic variation in fauna-habitat associations between regions due to biogeographic history, a large proportion may be predictable based on environmental context. The presence or absence of entire family level taxa can illustrate only broad differences in the use of mangroves, and is likely to conceal important species level differences between locations. That such large differences in habitat use are apparent, and are partly explainable by environmental context, highlights the primacy of these drivers for coastal ecosystem function. There were consistencies in mangrove utilisation in similar environmental contexts despite geographic separation, suggesting that divergent, context specific notions of habitat function are both valid and necessary. Habitat associations underpin our understanding of the requirements of fauna, and inform the way we manage the natural world. Due to the complex interplay of factors found in this study, it is important to consider the breadth of factors that define environmental context together, in order to understand habitat function. If the context-dependence of a habitat is properly understood, notions of its function for animals may be properly informed, enhancing our ability to make robust environmental decisions.

6 Habitat context predicts the use of mangroves by fishes



6.1 Introduction

The idea that organisms are constrained in their distribution by environmental context has long been a unifying concept in ecology (Grinnell 1917). The response of species to multiple interacting environmental gradients can determine their geographic distribution, and these responses define what is referred to as their 'fundamental niche' (Leibold 1995). Thus, an organism's distribution in multidimensional environmental space (sensu the hypervolume or realised niche, Whittaker et al. 1973) can predict their distribution in geographic space (Guisan and Zimmermann 2000). The requirements that fauna have for habitat, and a biogenic feature's tendency to fulfil those requirements, can also be shaped by the environment (Chapter 2). Using the same niche modelling approach, it is possible to determine the distribution of *habitat use* by certain fauna in geographic space, and use this information to construct a theoretical distribution in environmental space (Chapter 2, Figure 2.2), to produce predictive models of habitat use based on environmental context.

Fauna-habitat relationships depend on a range of contextual factors. Physical conditions are important in determining an animal's physical refuge requirements (Bain et al. 1988), and physiological tolerances can limit access to otherwise suitable habitat when physical conditions are unfavourable (Hasler et al. 2009). Similarly, ecological context can determine an animal's need for refuge from predation (Turner et al. 1999, Laundré et al. 2010), and the tendency of a habitat type to provide appropriate resources, such as food (Davis et al. 2014). Spatial and temporal context can shape the community using a habitat (Turner 1989, Boström et al. 2011), by determining connectivity between habitats through the movement of fauna (Lundberg and Moberg 2003), or through spatial subsidies (Polis et al. 1997). As a

consequence, there is substantial variation in habitat use over small scales, such as within regions, and over large scales, such as between regions, that appears to be driven by variation in environmental conditions (Chapters 2, 4 and 5). While the influence of some of these factors is well understood in isolation, the interplay of different contextual factors is poorly understood. There can be numerous important factors at play in any particular location, and without knowledge of the relative importance of different drivers, and how they interact, we remain unable to confidently predict habitat use and habitat function. To properly understand context-dependence in habitat use, we need to move towards defining threshold values that can distinguish between locations where a relationship will and will not occur, across the multiple factors that impact habitat use.

Context-dependent models of habitat use are needed for an informed understanding of ecosystem functioning at any particular location. Many habitat types are widely recognised as performing critical ecological functions for animals, that in turn support ecosystem functioning. For instance, tree hollows provide nesting sites for woodland vertebrates (Gibbons et al. 2002), and mangroves provide nurseries for coral reef fish (Nagelkerken et al. 2000c). Without these habitats, the fauna that require them can become scarce (Cockle et al. 2011, Nagelkerken et al. 2017), which in turn can alter ecosystem function and resilience (Olds et al. 2012b). Human societies derive value from these ecosystems, and efforts have been made to incorporate these kinds of ecosystem supporting services into environmental decision making (Carpenter et al. 2009, Sanchirico and Mumby 2009). However, the role that biogenic structures like these play in ecosystems is not constant in all situations, and depends on complex interactions that are sensitive to variations in environmental conditions, as described above. Defining the contexts in which certain vegetation types or biogenic

structures perform critical roles, and the contexts in which they do not, remains a pivotal challenge to our understanding of ecosystem functioning.

Mangroves provide a useful system to study context-dependence, because, although several key ecological roles are attributed to them, the extent and patterns of use by fauna is known to vary according to environmental factors. Mangroves are considered an integral part of coastal and estuarine ecosystems as an important habitat for coastal and estuarine fish around the world (Blaber 2013, Whitfield 2017), but the direct use of the habitat by fish is still under debate (Sheaves et al. 2016, Sheaves 2017). Mangroves are also considered an important part of nearshore reef ecosystems, supporting key ecosystem functions that are linked to resilience (Olds et al. 2012b). Their use by reef fish is often related to specific life history strategies. Mangroves are used by adult reef fish (Fox and Bellwood 2011, Barnes et al. 2012), are important stepping stones in the bipartite life histories of reef fish that make ontogenetic migrations between brackish areas and reefs (Russell and McDougall 2005), and are important nursery habitat for reef fish that do not utilise brackish areas (Mumby et al. 2004). However, the use of mangroves can vary widely (Kimirei et al. 2011, Sheaves 2012, Castellanos-Galindo et al. 2013). Mangrove use may vary at the regional level, according to climate and tidal regime (Igulu et al. 2014, Castellanos-Galindo and Krumme 2015), and across landscapes, according to qualities of the surrounding seascape (Pittman et al. 2007), and where mangrove habitat is positioned in that seascape (Dorenbosch et al. 2007). Local patch-scale factors are also important determinants of mangrove use, particularly water quality (Ley et al. 1999) water depth (Ellis and Bell 2004) and substratum (Blaber and Milton 1990, Barnes et al. 2012), all of which are in some ways the product of regional (e.g. climate and tide) and landscape factors.

How these various factors shape fish communities could be related to differences in the way that species use their environment. The value of any natural structure as habitat is likely to be specific to the functional ecological roles that a species fills. The value of mangroves as fish habitat is hypothesised to be due to the goods and services that mangroves provide, primarily food and refuge (Nagelkerken et al. 2008, Nagelkerken 2009b). For both reef and estuarine-coastal fish species, mangroves are considered rich foraging grounds (Rodelli et al. 1984, Sheaves and Molony 2000, Guest and Connolly 2005, Lugendo et al. 2006, Verweij et al. 2006), and important refuge sites (Laegdsgaard and Johnson 2001, Huijbers et al. 2011). The feeding potential and refuge potential of mangroves might vary with context (Lugendo et al. 2007b, Kimirei et al. 2015), and any variation will also determine what kinds of fish (e.g. herbivores vs zoobenthivores, small fish vs large fish) can derive value from mangroves.

The wide variation in the use of habitat by fauna means that we do not know where and when fauna-habitat relationships are important, and the role that certain habitat features play in ecosystems. The first step in understanding the context-dependence of these roles is to understand in which contexts certain types of fauna are predictably present or absent – i.e. their distribution in contextual space. In this study, I define the contexts in which various inshore-user groups (coastal-estuarine fish, brackish tolerant reef juveniles, marine tolerant reef juveniles, and adult reef fish) are present in mangrove habitat. I also explore how this relates to variation in functional ecological groups (defined by diet type and body size - henceforth referred to as 'eco-functional groups') in mangrove habitat. While simple presence of individuals, species, or functional groups does not necessarily demonstrate function of a particular habitat (e.g. nursery function; Beck et al. 2001), presence is a

necessary pre-condition for the performance of these functions. From this we can examine the distribution of habitat use in environmental space, and use this information to define threshold values that distinguish between locations where particular fish-habitat relationships are maintained and where they break down.

In this study, I examine the potential context-dependence in the presence of different fish functional groups in mangroves across the Indo-Pacific, based on a range of factors determined as important in previous studies (tide, reef proximity, salinity, depth, substratum and geomorphology – for details see Table 5.2). In order to minimise any influence of structural habitat qualities on models of context-dependence, I have focused entirely on *Rhizophora* prop-root mangrove habitat, a common and widely studied mangrove habitat (Nagelkerken et al. 2008). In determining context-dependence, I examine the relative importance of different contextual factors, and how they interact. With this information, I define the contextual thresholds for the use of mangrove habitat by different fish functional groups.

6.2 Methods

6.2.1 Study sites

Study sites throughout the Indo-Pacific at similar tropical latitudes were chosen to represent the breadth of variation present in environmental contexts inhabited by *Rhizophora* mangroves (Figure 6.1). Regions represent almost the full range of variation in tidal amplitude experienced in the Indo-Pacific, from 0.5 m in Polynesia to 11 m in North West Australia. *Rhizophora* mangroves were sampled in a range of different locations to cover the variation in environmental contexts within each study region. This range differed in each region (Table 6.1), due to differences in climate and geomorphology, as well as the relative dominance of *Rhizophora* mangroves. For example, in New Britain, *Nypa fruticans* dominated in brackish estuaries that extended far inland (i.e. far from coastal reefs), whereas in North East Australia *Rhizophora* mangroves were abundant in brackish estuaries far from reefs. These sampling imbalances reflect natural variation in environmental context. This unavoidably confounds extremes in particular variables with region, and this was considered during analysis and interpretation.

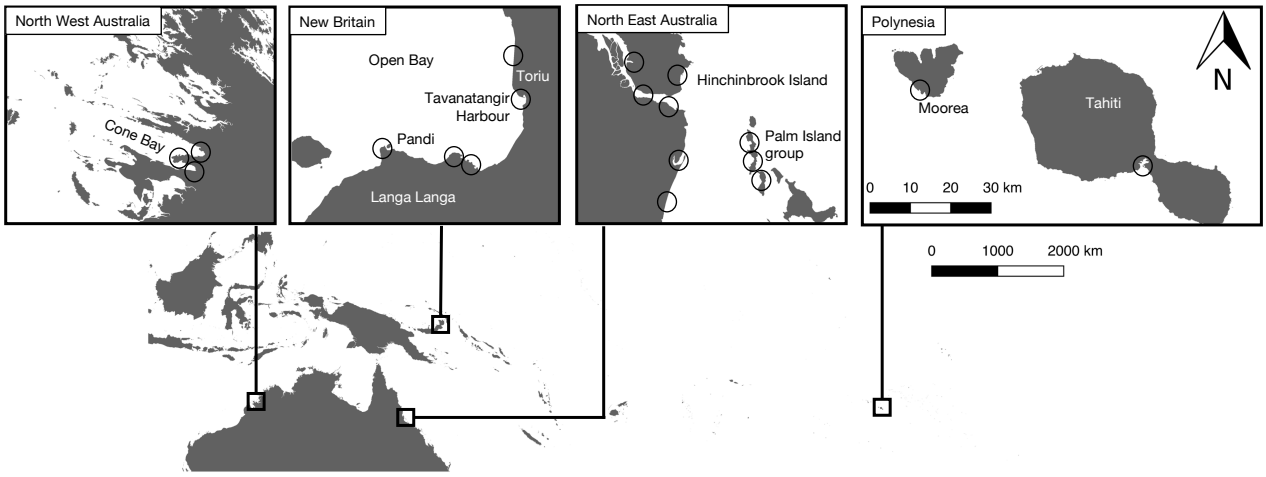


Figure 6.1 Distribution of sampling effort.

Top panel displays each of the four study regions. Within each map, black circles show the location of video sampling sites. Each map is identically scaled and oriented (scale bar located in French Polynesia map). Lower panel displays the eastern Indo-Pacific, and location of each study region.

Table 6.1 Regional sampling details of *Rhizophora* video samples, including environmental parameters and associated meta-data.

Climate data from www.climate-data.org, accessed October 2018. Tidal pattern data from data.shom.fr, accessed October 2018.

Region	Tidal range	Tidal pattern	Sampling period	Climate, yearly average rainfall.	Salinity: range sampled	Distance to reef: range sampled	Coordinates
Polynesia (French Polynesia)	0.5m	Semi-diurnal with diurnal inequality	October 2017	Tropical monsoon climate, 1800mm	34-32ppt	30m-360m	17° S 149° W
New Britain (Papua New Guinea)	0.9m	Mixed	September – November 2015 & 2016	Tropical monsoon climate, 3700mm	19-35ppt	30m-2.4km	4° S 151° E
North eastern Aust.	3.9m	Semi-diurnal with diurnal inequality	June – December 2014 & 2015	Tropical monsoon climate, 2237mm	14-35ppt	30m-25km	18° S 146° E
North western Aust.	10.8m	Semi-diurnal	June 2017	Tropical semi-arid climate, 562mm	34-35ppt	200m-8km	16° S 123° E

6.2.2 Remote Underwater Visual Census

All video surveys were conducted in prop-root habitat of mangroves of the genus *Rhizophora*, and all surveys were within the first 2 metres of the seaward edge of the forest. Video deployments were conducted as per the methods described in Chapter 3 Section 3.3.1, and footage was processed as described in Chapter 3 Section 3.3.2. This produced 297 video samples for analysis. As in Chapter 5, presence-absence data was used in the following analyses, as both schooling and solitary species could be encompassed within a single functional group, making abundance data non-comparable.

6.2.3 Functional categorisation

Fish detected in Remote Underwater Visual Census (RUVC) were identified to the lowest taxonomic grouping possible, and where possible, juvenile stages were differentiated from adult stages, as per the methods described in Chapter 3, Section 3.3.2. I then classified this data based on two different functional classification schemes described below. Information for functional categorisation of each species was gathered via Fishbase (Froese and Pauly 2018), refined using relevant species guides (Allen 1985, Allen et al. 2012) and primary research (Newman and Williams 1996, Baker and Sheaves 2005, Baker 2006) and further supplemented by relevant experts (Baker pers. comm, Sheaves pers. comm, Hemingson pers. comm.).

6.2.3.1 Classification scheme for inshore-user groups

I examined two distinct sets of fauna which use inshore areas differently – coastal-estuarine fish which do not move to reefs as adults, and reef fish, which are found on reefs during their adult phase. Given the life history specificity of the role of mangroves for reef fish, I assessed adults separately from juveniles. I also distinguished between reef juveniles based on their use of inshore areas. I assessed brackish-tolerant reef juveniles separately from marine-exclusive reef juveniles.

I used a simple classification scheme to assign different life-stage and taxonomic categories to inshore-user functional groups (see Appendix C, Table AC1). The 'coastal-estuarine fish' group were species that had a reported association with coastal-estuarine areas and no reported association with coral reefs throughout their life-history. The 'adult reef fish' group were fish that were visually identified as adults in RUVC that had a reported association with reef habitat during their adult phase. The 'marine juvenile reef fish' group were fish that were visually identified as juveniles in RUVC that had a reported association with reef habitat and that were not known to use brackish areas. The 'brackish tolerant juvenile reef fish' group were fish that were visually identified as juveniles in RUVC that had a reported association with reef habitat during adult life phases, and that were known to use brackish areas.

6.2.3.2 Classification scheme for eco-functional groups

In a separate set of analyses, I examined patterns of variation in eco-functional groups.

As taxa included both estuarine and reef associated fishes, I used a simplification of ecological functional groupings developed in estuarine (Elliott et al. 2007) and reef (Mouillot et al. 2014) settings to define fish into functional groups reflecting broad distinctions in ecological roles (see Appendix C, Table AC2). Both diet and body-size were used to construct these groupings. Diet reflects the food resource requirements of a species, and body size is known to be a useful indicator of the scale at which an animal exploits resources, such as the size of prey (Scharf et al. 2000), and spatial scale of foraging and refuge (Nash et al. 2013, Nash et al. 2014a).

Diet was used to assign species and life-stages into the following six trophic categories: planktivore, herbivore, zoobenthivore – sessile prey, zoobenthivore – mobile prey, omnivore and piscivore (defined as preying on fish and/or large invertebrate nekton).

Known maximum length was used to assign individuals into two size categories; small (0-15cm) and large (>15cm). Maximum size metrics provide a good general summary metric for fish, as mean metrics are difficult to obtain and prone to large local intra-specific variation (Nash et al. 2014b). Maximum length as reported on Fishbase (Froese and Pauly 2018) was used. If the life-history stage of an individual was identified during video analysis (Chapter 3, Section 3.3.2), then individuals were classified into the taxa specific maximum length of their particular life-stage. Adults were classified based on maximum length of the species. Juveniles were classified based on maximum length of juvenile phase for their taxonomic group. If length at maturity was available, this was used to place juvenile stages into maximum size categories. If not, a third of the maximum adult length was used as the estimated length at maturity (Nagelkerken and Van der Velde 2002). Early juvenile stages were assigned a maximum length based on available literature and unpublished data from fish collections associated with the project.

6.2.4 Predictors: Contextual variables

A range of different environmental predictor variables were used to examine context-dependence by different mangrove-associated fish functional groups. These have been summarised for quick reference (Table 6.2) and further details are provided below.

Table 6.2. Factors used in Random Forest analyses of fish functional group presence.

Factor	Description	Method	Unit	Hypothesis
Salinity	Salinity value of site during sampling period	Measured via conductivity or refractometry (for details see Chapter 5, Section 5.2.3.1)	parts per thousand (ppt)	Fish may be restricted in their use of habitat based on specific salinity tolerances or preferences (Harrison and Whitfield 2006, Whitfield et al. 2006).
Distance to reef	Shortest path between video sample and the closest patch of reef	GPS position and satellite imagery (for details see Chapter 5, Section 5.2.3.2)	log metres	The use of mangroves by reef fish may depend on their ability to access reef habitats, either daily or within their life-cycle, and this may be constrained by distance (Dorenbosch et al. 2007, Pittman et al. 2007, Jones et al. 2010).
Relative tidal height	Tidal height at the time of sampling as a proportion of the region's maximum tidal range	Calculated from hourly raw tidal height values (see text).	proportion	The use of mangroves by fish may depend on tidal height (Ellis and Bell 2008, Castellanos-Galindo and Krumme 2015). This provides a measure of tidal height that is equivalent between the various regions in our dataset.
Daily tidal range	Tidal amplitude during the sampling date	Daily tidal range was calculated for each sample from hourly raw tidal height values (see text).	metres	The use of mangroves by fish may depend on magnitude of tidal movement, both in terms of hydrological energy and access to the forest (Sheaves 2005). This value provides a quantitative measure of the magnitude of tidal movement on the day of sampling.
Geomorphology	Location of survey: channel (e.g. tidal channel, riverine channel) or coast (e.g. coastline of a bay, back reef)	GPS position and satellite imagery	categorical	Fish might use mangroves differently in channelized landscapes (Boström et al. 2011) compared to coastlines due to differences in amount of connected edge and access to the open water.

Substratum	Categorization of substratum using three categories; rock, sand and mud.	Visual assessment (see Chapter 3, Section 3.3.2)	categorical	Differences in substratum can influence the quality and quantity of invertebrate prey in the forest (Hsieh 1995), and therefore may affect the feeding potential of mangroves.
Depth	Vertical distance from the water surface to the bottom of the camera base at the time of sampling	Acoustic depth sounder or taught rope length during camera retrieval	metres	Water depth can restrict access to mangrove habitat based on fish body depth or behaviour. This could determine both the presence of individuals themselves, and by excluding their predators at shallow depths, determine the refuge value of mangrove habitat (Ellis and Bell 2004). This variable provides a measure of forest inundation independent of tidal state.
Region	The region in which the survey was taken	Location	categorical	Regions differ in tidal amplitude, which may lead to different habitat use strategies (Igulu et al. 2014). Regions also differ in climate, geomorphology, distribution of *Rhizophora* mangroves and biogeographic history. Regional distinctiveness may or may not relate to local scale environmental context. Regional scale responses, when compared to responses to other factors, and their relative importance, will aid in distinguishing biogeographic drivers from contextual effects on mangrove fish fauna.

6.2.4.1 Measurement of tidal variables

Measurements of tidal variables were derived from tidal gauge data recorded at the time of sampling, obtained from Australia's National Tidal Centre and University of Hawaii's Sea Level Center (Caldwell et al. 2015) for all locations except New Britain and North West Australia, where no tidal gauge networks exist proximal to our study sites. In these location, Australian Hydrographic Service tidal predictions (A.H.S. 2015, 2016, 2017) were used, verified by an array of underwater pressure loggers deployed in our study zone to detect any realised differences from these tidal predictions. In Papua New Guinea, loggers were

deployed in the lower reaches (300 - 1200 m from the mouth) of the Langa Langa, Pandi and Toriu systems, effectively covering the full breadth of our study zone - Open Bay (see Figure 6.1). The results showed no substantial departures from predictions at any location (i.e. high and low tide within 30 min of predicted for Tavanatangir Harbour). In the Kimberley (North Western Australia), loggers were deployed within Cone Bay (see Figure 6.1). Again, the results showed no substantial departures from predictions at any location (i.e. high and low tide within 30 min of predicted for Port Usborne). In upstream sites in Hinchinbrook Channel (North Eastern Australia) where known tidal lags exist, tidal values were calculated based on these lags (Wolanski et al. 1990).

6.2.5 Statistical analysis

6.2.5.1 Random Forest classification

I used Random Forest classification, a high-accuracy machine learning technique, to determine variable importance and model the relationship between contextual variables and inshore-user functional groups. Random Forest is a non-parametric statistical classifier that employs classification trees to partition data into homogeneous subgroups using predictor variables, until no further reduction in group heterogeneity can be achieved (Breiman 2001). Random Forest grows many trees, each with a randomised subset of data and predictor variables, and then tests each tree with the observations in the respective excluded data (out-of-bag (OOB)). Aggregating the proportions of OOB predictions across the entire 'forest' of trees allows for the estimation of probability of class membership based on predictor

variables without the dangers of over-fitting associated with single trees. The contribution of each variable to model accuracy (variable importance) is determined by comparing the misclassification rates when using actual and randomly permuted values for each predictor variable (Cutler et al. 2007). To visualize the relationship between predictor variables and the response variable, I used the feature contribution method (Palczewska et al. 2014), which extracts the influence of the variable of interest on the class prediction for each observation from the Random Forest model.

To examine context-dependence in the presence of each inshore-user functional group, I built a Random Forest model for each inshore-user group, calculating variable importance and the feature contributions of each contextual variable. Using binary presence-absence data of the inshore-user group as the classifying factor, Random Forests of 5000 trees were grown, weighted by the prior proportion of presence vs absence. For each Random Forest, the OOB error rates were calculated to evaluate model fit, and variable importance was calculated using the permutation process described above. Feature contributions were calculated for each predictive variable, however, only the two most important variables were selected for interpretation to avoid the use of variables that contribute little to model accuracy. In feature contribution plots, the influence of the predictor variable on class prediction (presence or absence of the inshore-user group) was displayed for each observation, along with an average for each value of the contextual variable to aid visualisation of the relationship, from which goodness of fit was calculated (Welling et al. 2016).

All analyses were performed using R version 3.3.3 (R Core Team 2017). Random Forests were built using the 'randomForest' package (Liaw and Wiener 2002), and feature contribution plots were displayed with the 'forestFloor' package (Welling et al. 2016).

6.2.5.2 Mangrove community functional composition

To investigate how the functional group composition of assemblages varied according to context, multidimensional scaling (MDS) was performed for both inshore-user group composition, and eco-functional group composition. In both analyses, for each sample, the taxonomic richness (i.e. count of different taxa) within each functional group was calculated. These values were compared between samples by constructing a dissimilarity matrix using the Bray-Curtis similarity coefficient. To display these patterns graphically for interpretation, multidimensional scaling was performed, using the 'metaMDS' function in package Vegan (Oksanen et al. 2013) in R. The 'envfit' function in package Vegan was used to fit contextual variables (Table 6.2) to the ordination space. Region was not included in the environmental fitting procedure as this information was displayed by colour coding individual points in the final output. Results from these analyses were displayed using the 'ggplot2' package (Wickham 2016).

6.2.5.3 Data visualisation

To examine how eco-functional groups were distributed relative to contextual variables identified as important in multivariate analysis, circle plots were constructed showing the

proportion of each group at each point throughout the contextual space, relative to the magnitude of sampling effort. Similarly, to visualise the context-dependence of different inshore-user groups, 2 dimensional contextual spaces were constructed based on the most important variables for each group, as identified in Random Forest analysis. The threshold values for each group identified in Random Forest analysis were used to draw contextual limits for each group's association with mangrove habitat. The distribution and magnitude of sampling across this space was illustrated using circle plots, again this was displayed using the 'ggplot2' package (Wickham 2016) in R.

6.3 Results:

6.3.1 Thresholds in inshore-user group association with mangrove habitat

Radom forest models were able to predict the presence or absence of each inshore-user group, with all models achieving an Out Of Bag (OOB) error rate of less than 35%.

6.3.1.1 Coastal-estuarine fish

Region was the most important variable in predicting the presence of coastal-estuarine fish in mangroves (Fig. 2a). This group tended to be absent in samples from Polynesia (see Appendix C, Figure AC1). In other regions, the use of mangroves by coastal-estuarine fish appears context dependent. Salinity and distance to reef were the most important contextual

predictors for coastal-estuarine fish (Fig. 2a). The Random Forest model, which was successful at predicting the presence or absence of coastal-estuarine fish, used salinity values of between 14 and 28 ppt to predict their presence (Fig. 2b). This means that this group was predictably present in mangroves between salinities of 14 and 28 ppt. At salinities above these values, their presence in mangroves appears unpredictable. This group was predictably absent from mangroves less than 125m from reefs, and their presence was highly variable in mangroves further from reefs (Fig. 2c). Due to the uneven distribution of contexts throughout the Indo-Pacific (see Appendix C, Figure AC6), this group's absence from forests in Polynesia is confounded with its response to contextual factors, with Polynesia lacking extensive areas of *Rhizophora* forest below 32ppt and >150m from reefs.

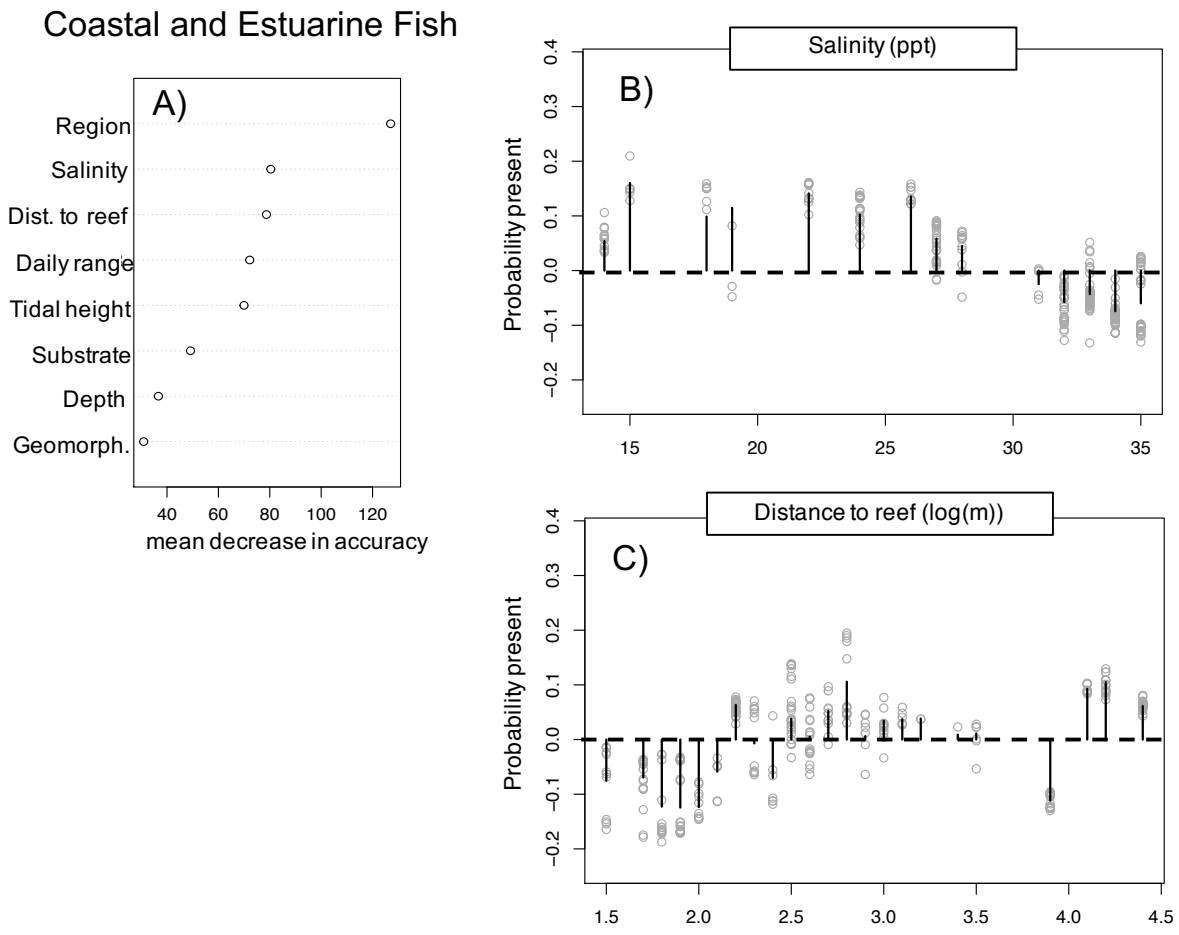


Figure 6.2 Summary of Random Forest prediction model of coastal-estuarine fish presence in mangrove habitat.

Variable importance, measured as the mean decrease in model accuracy when a variable is removed from the model (left panel), and the feature contribution plots of the most important contextual variables (right panel) are shown. In feature contribution plots, grey circles show the influence of the contextual variable on class prediction for each observation, and the length of black bars represent means, indicating the magnitude of positive or negative contribution for each value of the feature variable. Model OOB estimate of error rate: 18.52%. For all feature contribution plots in the model, see Appendix C, Figure AC1.

6.3.1.2 Adult reef fish

The distance of mangrove habitat from reefs was of overwhelming importance (more than twice that of any other variable) in predicting the presence of adult reef fish (Figure 6.3a). This variable made particularly high contributions to the Random Forest predictive model, with probability contributions ≥0.2 (Figure 6.3b). Adult reef fish were predictably present in

mangroves very close to reefs (≤2log(m), i.e. ≤100m), and tended to be present in mangroves less than 1km (<3 log(m)) from reefs. In mangroves further than 1.5km from reefs, there was a high probability that they would be absent. Daily tidal range was the second most important predictor (Fig. 3a), with adult reef fish generally present in mangroves experiencing tidal amplitudes of ≤ 1 m and absent from mangroves experiencing tidal amplitudes of ≥ 3 m (Fig. 3c).

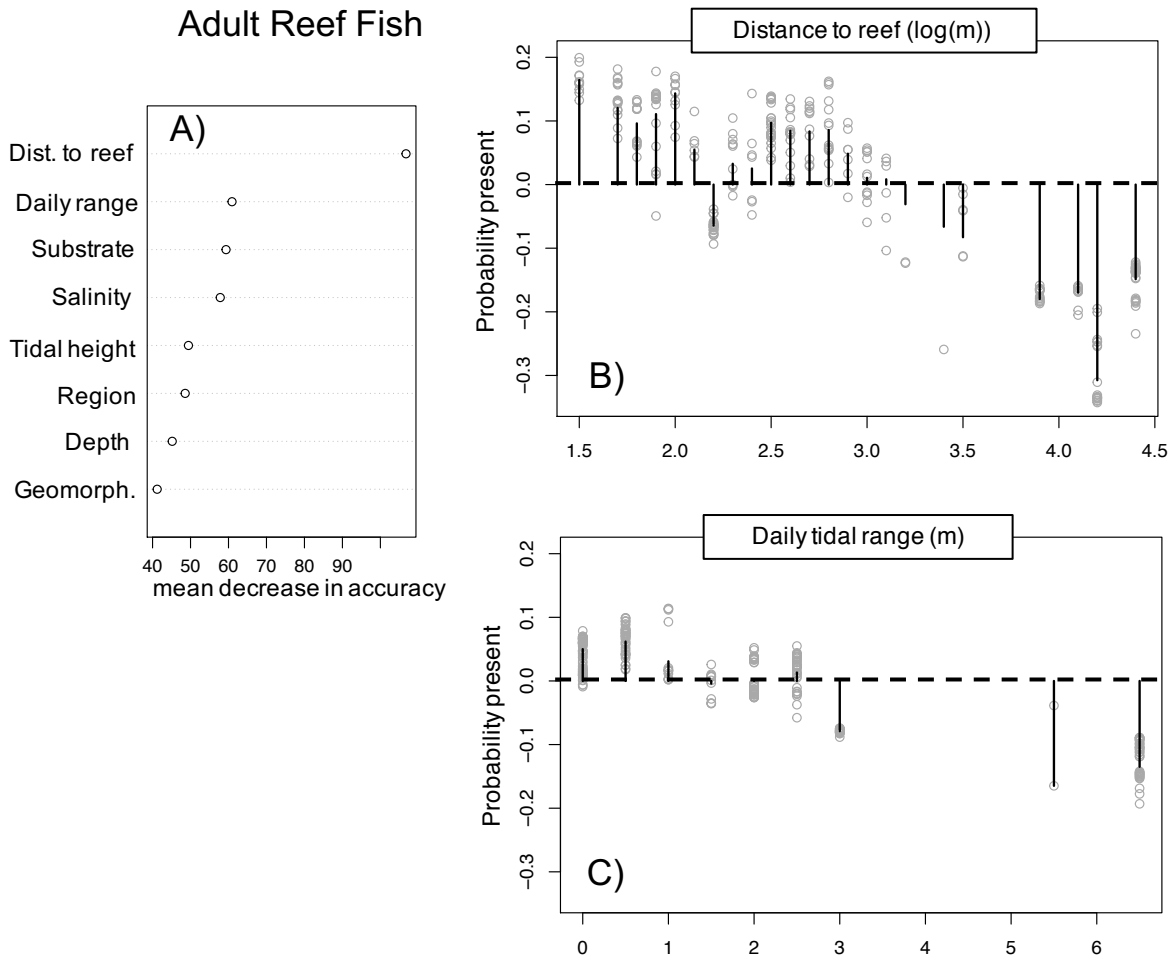


Figure 6.3 Summary of Random Forest prediction model of adult reef fish presence in mangrove habitat.

Variable importance, measured as the mean decrease in model accuracy when a variable is removed from the model (left panel), and the feature contribution plots of the most important contextual variables (right panel) are shown. In feature contribution plots, grey circles show the influence of the contextual variable on class prediction for each observation, and the length of black bars represent means, indicating the magnitude of positive or negative contribution for each value of the feature variable. Model OOB estimate of error rate: 25.25%. For all feature contribution plots in the model, see Appendix C, Figure AC2.

6.3.1.3 Marine juvenile reef fish

Region was the most important variable in predicting the presence of marine juvenile reef fish in mangroves, followed by daily tidal amplitude and distance to reef (Figure 6.4a). This group was predictably present in samples from Polynesia. Marine juvenile reef fish tended to be present in samples that experienced one metre or less of tidal movement on the day of sampling. This included samples from both Polynesia and New Britain. Between one metre and three metres daily tidal range, their presence was variable, and in samples three metres and greater they were predictably absent (Figure 6.4b). Additionally, marine juvenile reef fish tended to be present in mangroves between 50 and 150 metres from reefs. In mangroves further than 250m, they were predictably absent (Figure 6.4c). The maximum tidal amplitude experienced in the Polynesian sampling region is 0.5 metres (i.e. all samples are below this value), and most areas of *Rhizophora* forest are less than 150m from reefs, therefore every sample was within the contexts where marine juvenile reef fish were predictably present in New Britain, which had a much larger spread of contextual variation (see Appendix C, Figure AC6). Therefore, the importance of region is confounded with the groups response to daily tidal amplitude and distance to reef.

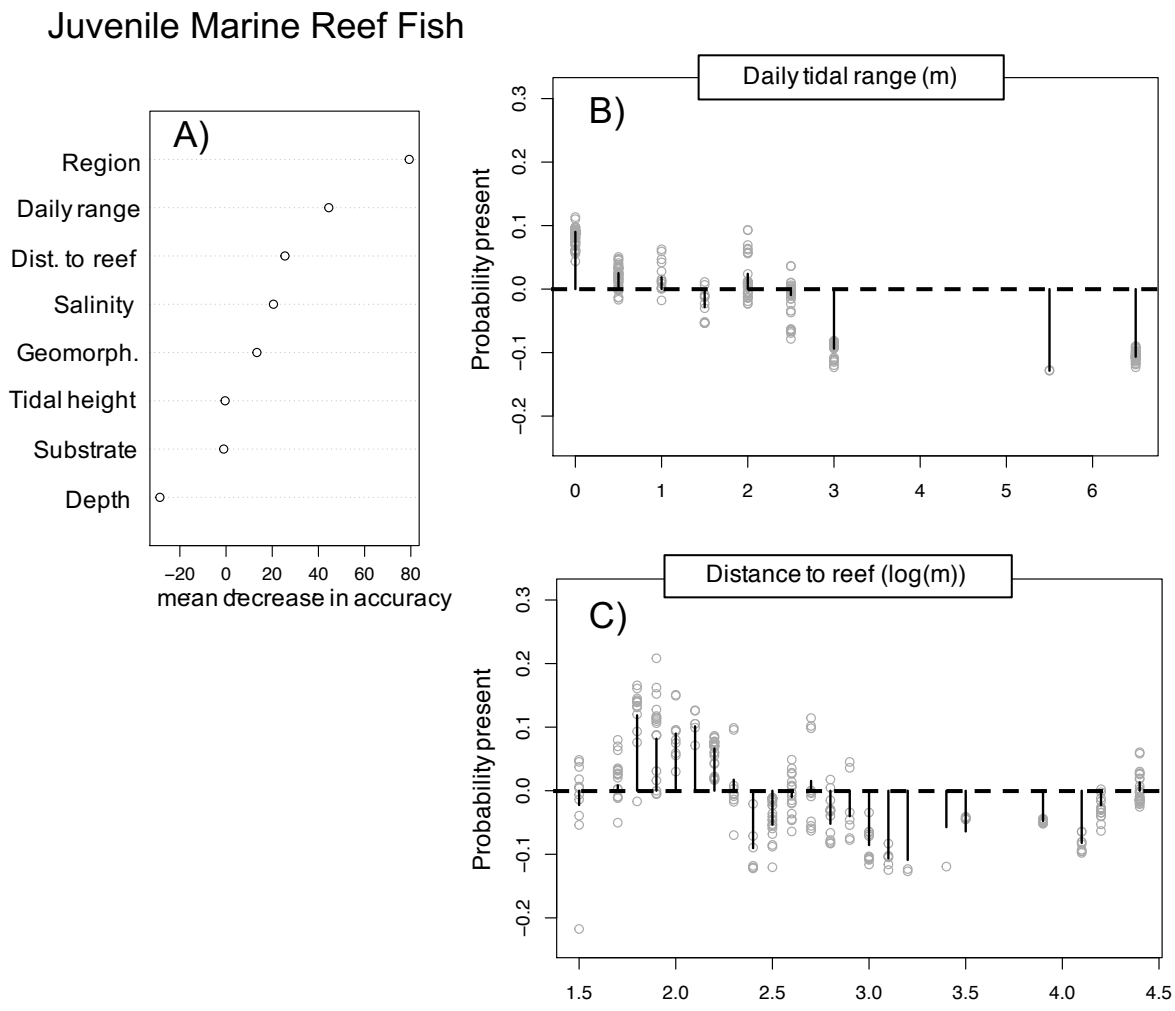


Figure 6.4 Summary of Random Forest prediction model of juvenile marine reef fish presence in mangrove habitat.

Variable importance, measured as the mean decrease in model accuracy when a variable is removed from the model (left panel), and the feature contribution plots of the most important contextual variables (right panel) are shown. In feature contribution plots, grey circles show the influence of the contextual variable on class prediction for each observation, and the length of black bars represent means, indicating the magnitude of positive or negative contribution for each value of the feature variable. Model OOB estimate of error rate: 33.67%. For all feature contribution plots in the model, see Appendix C, Figure AC3.

6.3.1.4 Brackish tolerant juvenile reef fish

Daily tidal amplitude and distance to reef were the most important predictors of the use of mangroves by brackish tolerant reef fish juveniles (Figure 6.5a). This group tended to be

present in mangroves that experienced less than three metres of tidal movement, and were predictably absent when tidal movement was three metres or higher (Figure 6.5b). They were reliably present in mangroves between 80m and 320m from the reef, and their presence at greater distances was variable (Figure 6.5c).

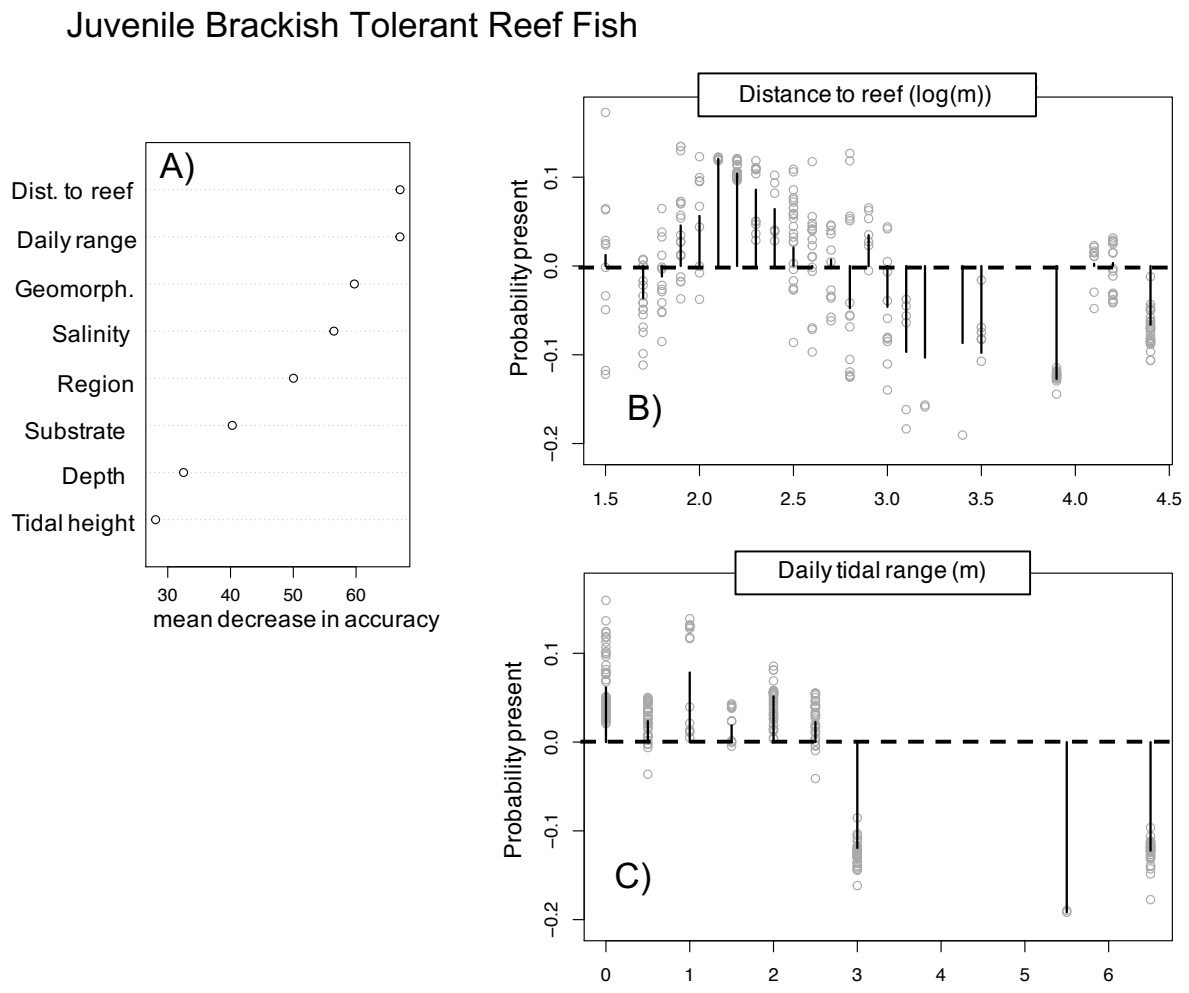


Figure 6.5 Summary of Random Forest prediction model of juvenile brackish-tolerant reef fish presence in mangrove habitat.

Variable importance, measured as the mean decrease in model accuracy when a variable is removed from the model (left panel), and the feature contribution plots of the most important contextual variables (right panel) are shown. In feature contribution plots, grey circles show the influence of the contextual variable on class prediction for each observation, and the length of black bars represent means, indicating the magnitude of positive or negative contribution for each value of the feature variable. Model OOB estimate of error rate: 31.65%. For all feature contribution plots in the model, see Appendix C, Figure AC4.

6.3.2 Inshore-user group composition of mangrove assemblages - potential contextual drivers

The inshore-user group composition of assemblages varied according to context. MDS ordination of samples revealed the broad contrast between sites dominated by reef fish user groups and those dominated coastal-estuarine fish, as well as the spread variation in species mix between those two extremes. The ordination appears to be strongly influenced by a substantial group of samples that only contained coastal-estuarine fish (Figure 6.6). As would be expected from the individual responses of user groups to contextual variables in Random Forest analyses above, context varied significantly across this ordination space (Figure 6.7). Samples dominated by reef fish were characterised by high salinities, small tidal amplitudes and small distances to reef. These samples were also more likely to be characterised by coastal geomorphology, and sandy substratums. Samples dominated by coastal-estuarine fish were characterised by lower salinities, higher tidal amplitudes and larger distances to reef. These samples were also more likely to be characterised by channelised geomorphology, and silty substratums. Depth of the sample and relative tidal height at the time of sampling were not substantially correlated with the ordination space. Overall, community responses to different contextual factors were correlated (Figure 6.7). Samples with increasing salinity values differed in assemblage composition in a directly opposing direction to samples with increasing values of distance to reef. In addition, samples with increasing tidal amplitude values differed in assemblage composition in a similar direction to samples with increasing distance to reef values. Therefore, it is difficult to disentangle the individual effects of each variable on assemblage composition.

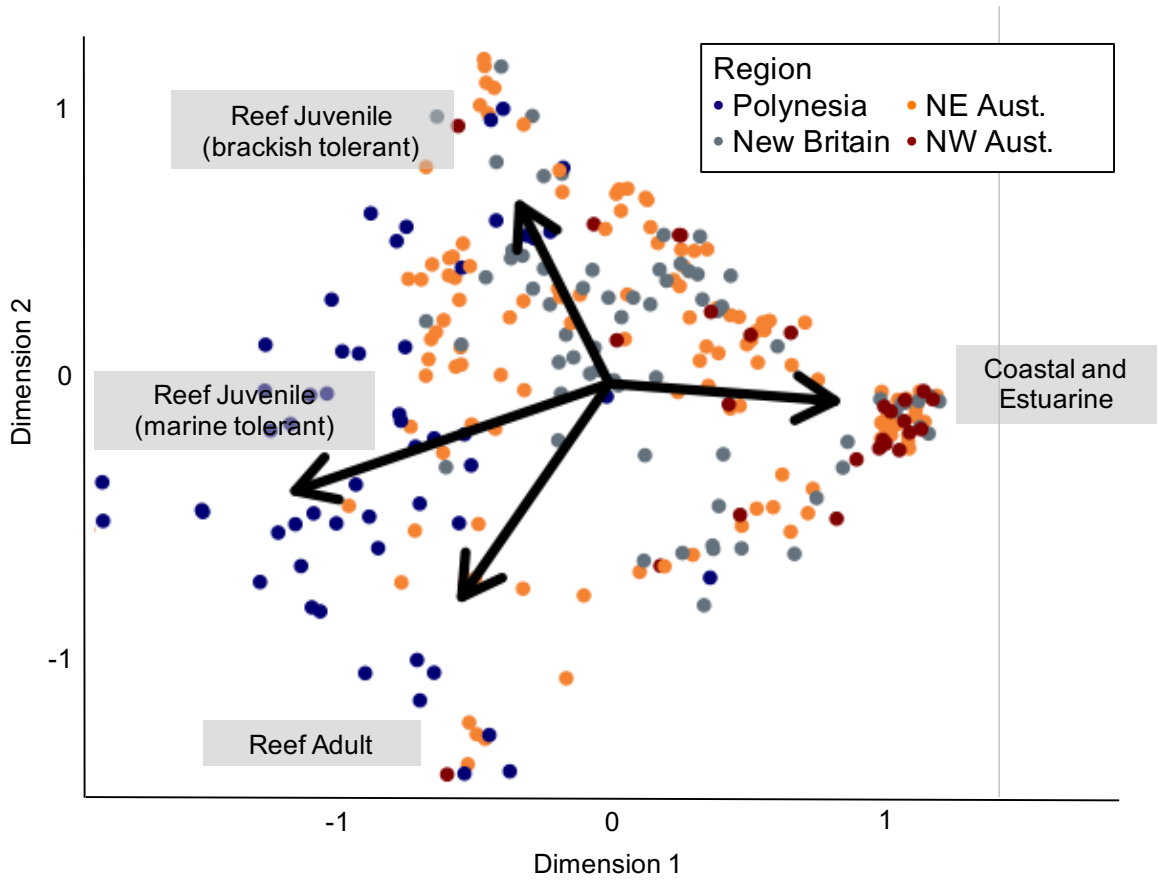


Figure 6.6 MDS ordination displaying a 2D solution (stress: 0.11) capturing the differences between samples based on inshore-user group assemblage composition (n=271).

Dimensional values are scaled such that a distance of one unit represents a halving of assemblage similarity between samples. Inshore-user group vectors represent the direction of positive correlation with the ordination space. Vector terminal position represents a user-group's centre of occurrence in the ordination space, calculated using the weighted average of sample abundances. Points have been jittered (at a scale of 0.1 on each dimensional axis) to reveal quantities of points occurring at identical positions in the ordination.

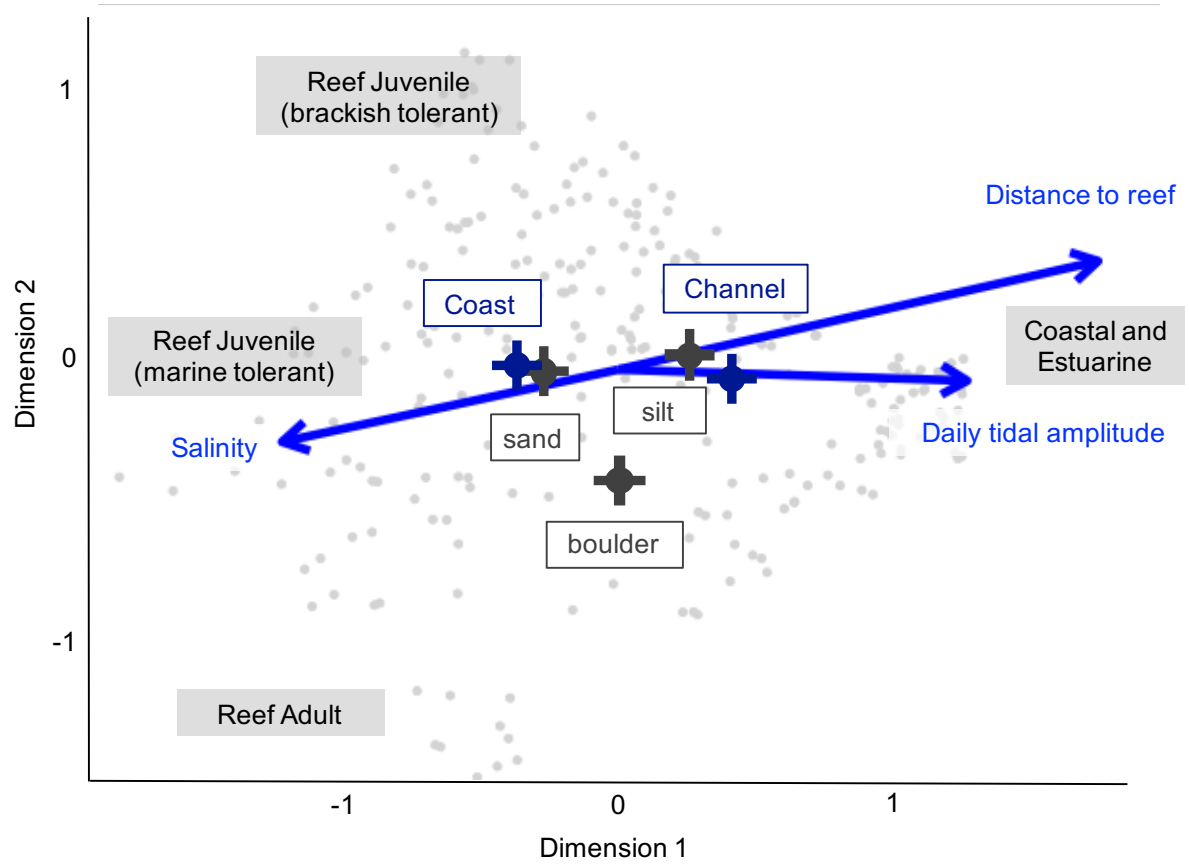


Figure 6.7 MDS ordination of inshore-user group assemblage composition as shown in Figure 6.6, with fitted contextual variables.

Only variables with a reasonable correlation with the ordination space ($r2 > 0.1$) are displayed. For categorical variables (geomorphology and substratum), centroids are shown for each category. For continuous variables, vectors are shown. Vectors represent the direction of positive correlation with the ordination space. Vector lengths are proportional to their r2 values, and are scaled to fit the ordination space.

6.3.3 Eco-functional group composition of mangrove assemblages - potential contextual drivers

There were clear patterns in the assemblage composition of eco-functional groups. These functional groupings were based on the diet and body-size of fishes. There was general distinction between samples dominated by large bodied zoobenthivores that prey on mobile invertebrates, samples dominated by small-bodied planktivores and zoobenthivores that prey

on mobile invertebrates, and samples containing a diversity of eco-functional groups (Figure 6.8). Context varied significantly across this ordination (Figure 6.9). Samples dominated by zoobenthivores that prey on mobile invertebrates were characterised by lower salinities, higher tidal amplitudes and larger distances to reef. Samples containing a diversity of eco-functional groups were characterised by high salinities, small tidal amplitudes and small distances to reef. Other contextual factors were not substantially correlated with the ordination space. Community responses to different contextual factors were correlated (Figure 6.9). Samples with increasing salinity values differed in assemblage composition in a directly opposing direction to samples with increasing values of distance to reef and tidal amplitude. As was the case for inshore-user groups, it is therefore difficult to disentangle the individual effects of each variable on eco-functional assemblage composition. The response of individual eco-functional groups to context is explored further in the Appendix (see Appendix C, Text AC1, and Figures AC6 and AC7). Overall, these patterns appear to be driven by the absence of a range of eco-functional groups in large tidal range, large distance from reefs, low salinity contexts. Zoobenthivores that prey on mobile invertebrates were widely distributed throughout all contexts, and it is the absence of other groups that drives the observed differences in assemblage composition. While there are similarities in the response of eco-functional groups to these three different factors, they appear to be acting somewhat independently. Large tidal ranges lack a diversity of eco-functional groups, even when salinity remains high and distance to reef remains low (see Appendix C, Figures AC6 and AC7).

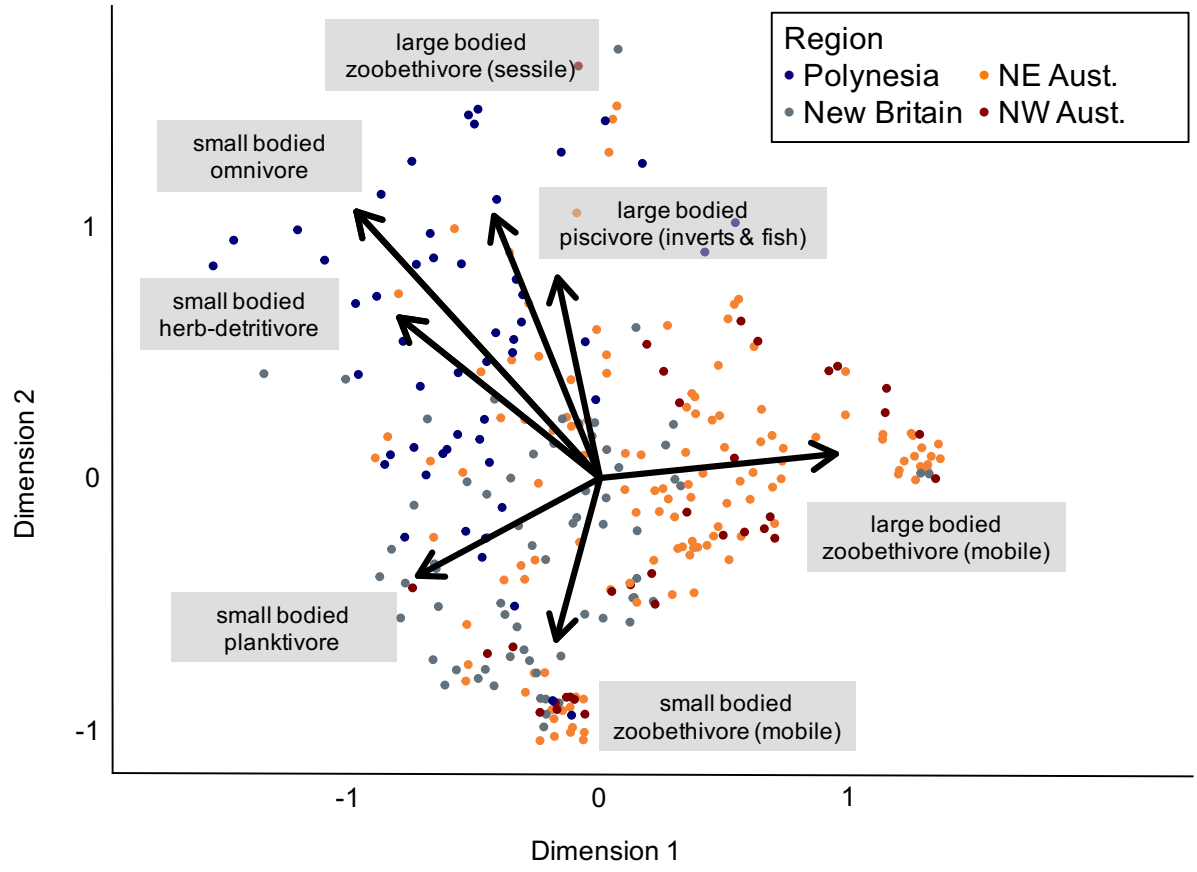


Figure 6.8 MDS ordination displaying a 2D solution (stress: 0.15) capturing the differences between samples based on eco-functional group assemblage composition (n=279).

Dimensional values are scaled such that a distance of one unit represents a halving of assemblage similarity between samples. Inshore-user group vectors represent the direction of positive correlation with the ordination space. Vector terminal position represents a functional group's centre of occurrence in the ordination space, calculated using the weighted average of sample abundances. Only functional groups that are far (>0.5 dimensional units) from the centre of the ordination space (i.e. taxa that differ strongly across the ordination space) are shown. Points have been jittered (at a scale of 0.1 on each dimensional axis) to reveal quantities of points occurring at identical positions in the ordination.

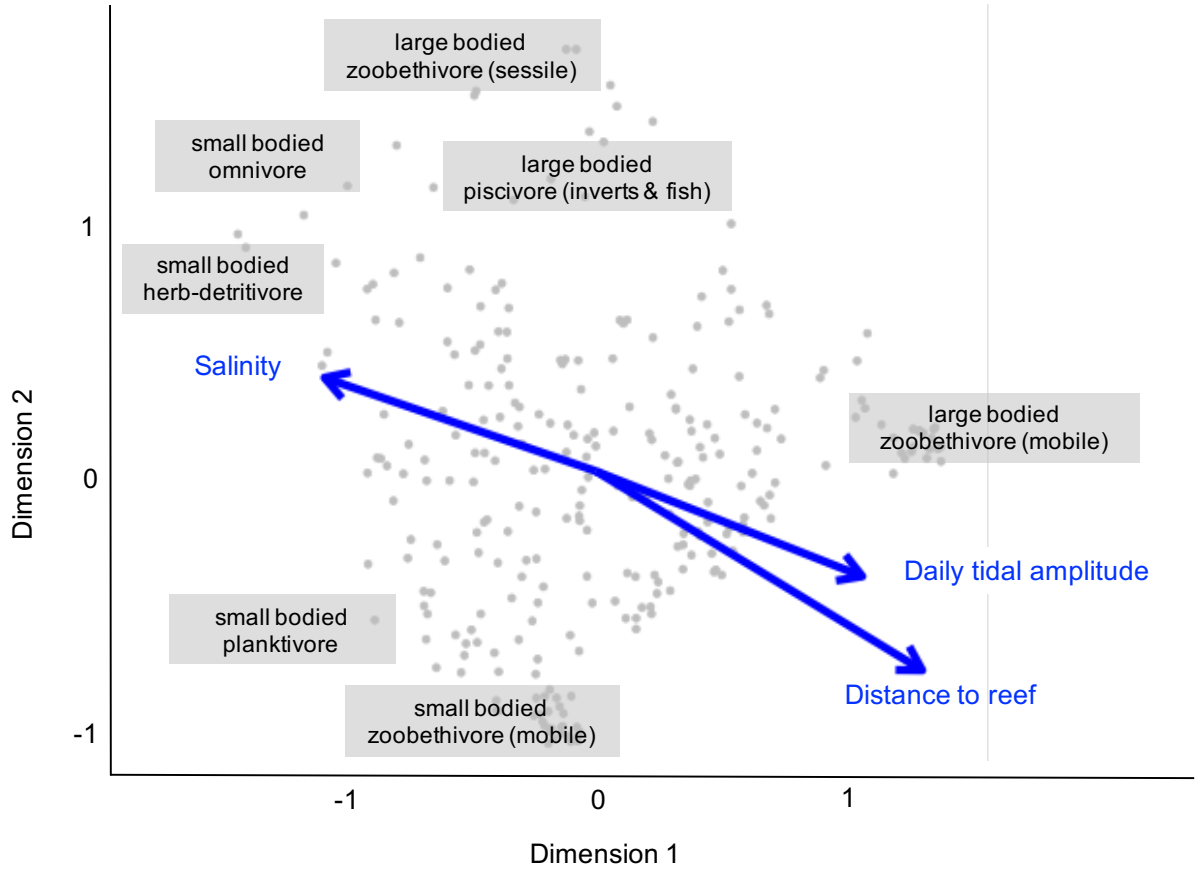


Figure 6.9 MDS ordination of eco-functional group assemblage composition as shown in Figure 6.8, with fitted contextual variables.

Only variables with a reasonable correlation with the ordination space ($r2 > 0.1$) are displayed. Vectors represent the direction of positive correlation with the ordination space. Vector lengths are proportional to their r2 values, and are scaled to fit the ordination space.

6.4 Discussion

The context of mangrove prop-root habitat determines how this habitat is used by fish. There were clear and unique contextual thresholds definable for each inshore-user group, reflecting strong context-dependence in the role of mangroves as habitat. Distance to reef and daily tidal range were important variables for all three reef fish groups, however, the threshold values for presence differed between each group (Figure 6.10). Salinity and distance to reef

were important predictors for coastal-estuarine fish (Figure 6.11). Together, these factors appear to drive broad functional differences in mangrove fish assemblages. There were marked similarities in the responses of inshore-user groups and eco-functional groups to contextual variation. Across the same contextual axes of tide, distance to reef and salinity, there was a profound difference in the fish that use mangroves, both in terms of inshore-user groups (coastal-estuarine vs reef), but also in terms of their eco-functional roles (high diversity vs zoobenthivore dominated). These contextual parameters, therefore, define the composition of mangroves fish assemblages across multiple functional axes, and point to an underlying functional difference in the way mangroves are used in reef versus coastal-estuarine ecosystems.

6.4.1 Important contextual factors:

It is difficult to distinguish the impact of individual contextual drivers on functional groups, due to their complex interactions. In the dataset used, independent variation in contextual factors was constrained by their natural distribution. Variation in salinity at locations close to reefs is constrained by the salinity tolerance of corals (Fabricius et al. 2005). At locations with large tidal ranges, distance to reef is generally constrained at its lower bounds by a lack of tolerance to tidal exposure in corals (Anthony and Kerswell 2007). As a result, salinity, tidal range and distance to reef are broadly correlated. However, the large spread of variation in contextual factors sampled at each location (see Appendix C, Figures AC5 & AC6) provide important exceptions to what would be expected from a co-linear response, such as the exclusion of a diversity of eco-functional groups from large tidal range locations regardless of distance to reef (see Appendix C, Figure AC7). This suggests that while these

factors often act in concert, fish will respond to individual contextual factors. Contextual factors were also constrained by geography (see Table 6.2). Context variables and region were confounded in Polynesia due to the uneven distribution of contexts throughout the Indo-Pacific. As stated in Chapter 5, the amphidrome point of the South Pacific lies far from any major landmasses (Luther and Wunsch 1975), meaning that the area with the smallest tidal range lacked extensive areas of both brackish *Rhizophora* and *Rhizophora* far from reefs. Therefore, it is difficult to separate the potential effects of biogeography and context in the importance of Polynesia as a powerful predictor in Random Forest analysis of the absence of coastal-estuarine fish, and the presence of marine reef juveniles. However, the response of fish to contextual variables within Polynesia are consistent with equivalent contexts elsewhere, suggesting that context is an important driver. Though more targeted research is required to disentangle the mechanism behind the contextual variation observed in this study, tidal range, distance to reef and salinity clearly interact to determine the use of mangroves by fish.

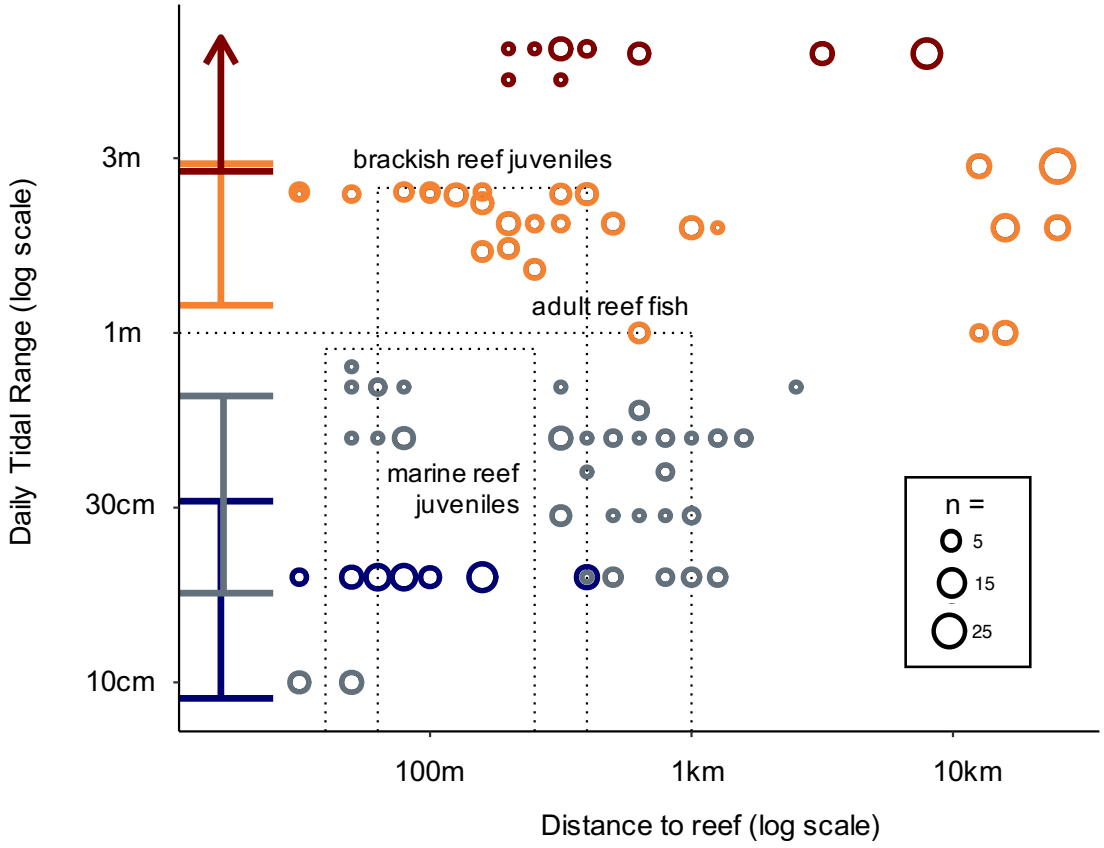


Figure 6.10 Contextual thresholds of daily tidal range and distance to reef for reef fish use of mangroves, with distribution of sampled range shown for each region.

Size of circles is proportional to the number of samples at that point in contextual space, and the colour of circles corresponds to region: dark-blue for Polynesia, grey for New Britain, orange for North Eastern Australia, and red for North western Australia. Brackets (also coloured by region) on the left hand side of the graph depict the spread of daily tidal ranges experienced in each region, excluding the maximum and minimum 10%, to show the spread of daily ranges usually experienced in each region.

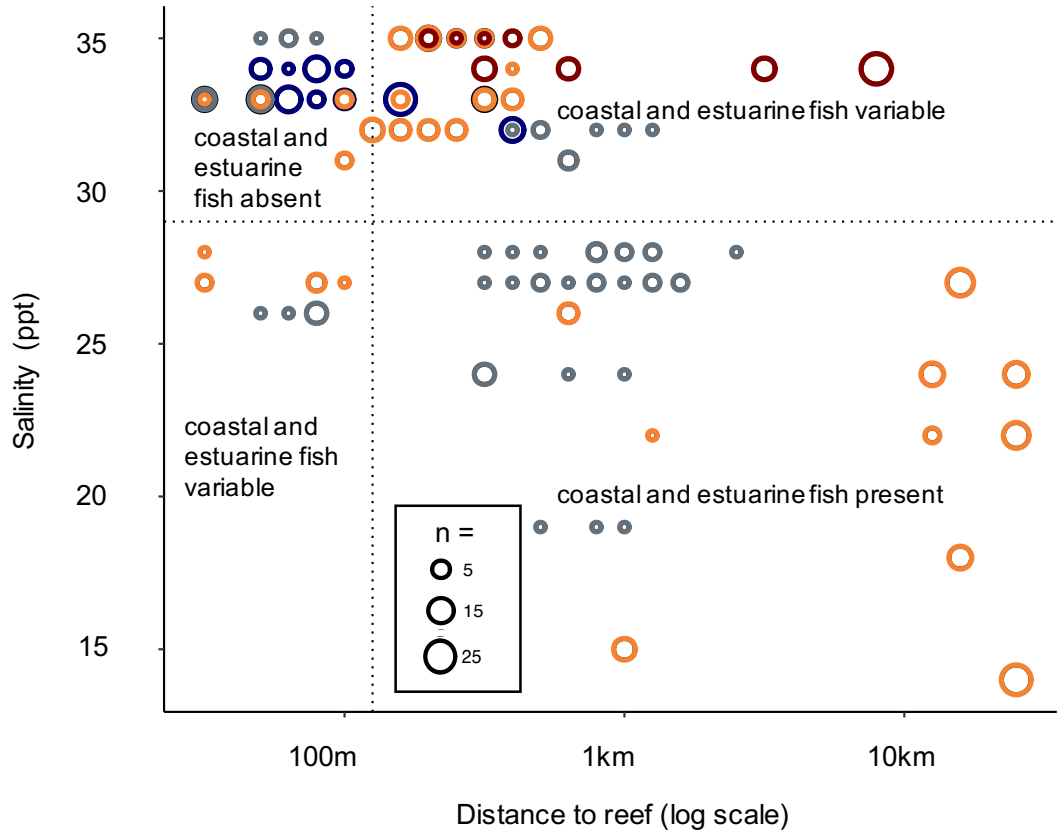


Figure 6.11 Contextual thresholds in mangrove presence for coastal-estuarine fish, with distribution of sampled range shown for each region. Size of circles is proportional to the number of samples at that point in contextual space, and the colour of circles corresponds to region: dark-blue for Polynesia, grey for New Britain, orange for North Eastern Australia, and red for North western Australia.

6.4.1.1 Tidal range

Tidal range appears to be a crucial determinant of the presence of reef fish. Tidal range was responsible for a large proportion of the predictive power in models for juveniles, and both adults and juveniles were predictably absent in large tidal range contexts. These findings are consistent with the results of a recent global meta-analysis (Igulu et al. 2014), that found a lower tendency for reef fish juveniles to use mangroves in larger tidal range contexts, relative to two alternative subtidal habitats – reefs and seagrass. In addition many eco-functional groups appear to be excluded from large tidal range contexts. For many fish, the magnitude

of tidal movement may determine the use of mangroves by altering the balance between the benefits of inhabiting mangroves, and the challenges of performing intertidal migrations. Tidal amplitude determines access to mangrove forests in a number of ways, and this has a range of consequences for fish (Sheaves 2005). Firstly, it determines the depth and duration that mangroves are inundated and available to fish (Baker et al. 2015) and the proportion of time fish must necessarily spend outside the forest. Secondly, it determines the depth of water in the mangroves, and the duration of flooding (Baker et al. 2015). Therefore, it will determine the duration of any shallow water derived refuge value (Paterson and Whitfield 2000, Rypel et al. 2007) obtained by utilising mangrove habitat. Thirdly, tidal amplitude will determine the magnitude of water movement through the forest. While mangrove structure provides refuge from tidal currents and wave energy (Brinkman et al. 1997, Mazda et al. 1997), with large enough tidal range, the hydrological forces experienced in the forest may eliminate any hydro-dynamic advantages of inhabiting mangroves relative to other intertidal habitats. Finally, tidal amplitude is known to regulate levels of dissolved oxygen and the duration of anoxic conditions inside mangrove forests, with larger tides resulting in larger fluctuations in oxygen, with obvious implications for fish (Mattone and Sheaves 2017). For fish that use reefs, the habitat value of mangroves in areas of large tidal ranges may be relatively low, and utilising it may come with greater risk of predation. In macro-tidal contexts, reef fish that are adapted to brackish coastal environments are perhaps equipped to cope with these challenges, and this could explain the difference in tidal range context-dependence between groups. Both juvenile reef fish that lack adaptations to brackish coastal environments, and adult reef fish (i.e. fish that primarily use reefs during their adult phase) have a lower tidal range threshold for mangrove use. Overall, any effect due to daily tidal range will always be bound up with regional differences in tidal regime, as macro-tidal regions will very rarely experience daily tidal ranges that overlap with micro-tidal regions

(Figure 6.10). In micro-tidal contexts, mangroves could provide a relatively stable, permanently submerged complex habitat that can be utilised by both juvenile and adult reef fish when proximal to reefs, without the challenges associated with more significant tidal forces.

6.4.1.2 Distance to reef

The distance between mangroves and reefs was important for every inshore-user group, but their responses were markedly different. For reef fish, being close to reefs was a key predictor of their presence in the mangroves. Estuarine fish, on the other hand, were negatively associated with distance to reef, using mangroves that were over a minimum threshold distance from reefs (≥125m). These patterns are probably due to the fact that very few fish are likely to solely use mangrove habitat during their lifecycle (Sheaves 2009). Therefore, the use of mangroves is likely to depend on proximity to other habitats that fish require, at scales relevant to their daily or ontogenetic movements (Nagelkerken et al. 2015). In the case of reef fish, their use of mangroves clearly depends on proximity to reef in some way, either directly through their requirements for reef habitat (Unsworth et al. 2008), or their general proximity to reef-flat or lagoonal habitats, which over the scales sampled in this study, would co-vary with proximity to reef. This might include appropriate settlement habitat such as coral rubble (Dahlgren and Eggleston 2000), or subtidal seagrass or macroalgae (Dorenbosch et al. 2007) that may be used in their utilisation of lagoonal nurseries as a whole (Chapter 4, Bradley et al. 2019). On the other hand, coastal-estuarine fish might require access to habitats such as coastal rocky reef or estuarine seagrass (Bradley et al. 2017), that would generally be far from reefs. In general, mangroves close to reefs are

likely to be in the correct mosaic of habitats used by reef fish, and therefore, less likely to be in the kind of mosaic used by coastal-estuarine fish.

6.4.1.3 Salinity

Salinity was a powerful predictor of the use of mangrove habitat by coastal-estuarine fish. Mangrove habitat in brackish salinities (i.e. <30ppt, following Por 1972), reliably contained coastal-estuarine fish. Mangrove habitat in euhaline waters (i.e. 30-36ppt, following Por 1972), tended not to contain coastal-estuarine fish, with some variability. Salinity appears to predict the presence of coastal-estuarine fish independent of distance to reef. Brackish mangroves close to reefs (e.g. <200m) frequently contained coastal-estuarine fish (Figure 6.11). Likewise, in marine mangroves far from reefs (e.g. >350m) coastal-estuarine fish occurred far less frequently than in lower salinity mangroves at similar distances (Figure 6.11). For reef fish, salinity was consistently much less important than other predictors (Figures 6.3a, 6.4a and 6.5a). Salinity gradients are known to be important determinants of mangrove communities at the scale of individual systems (Ley et al. 1999, Barletta et al. 2005). Our findings suggest that at global scales, coastal-estuarine fish are consistently found in brackish salinity mangroves (Harrison and Whitfield 2006) whereas for reef fish, even those with defined salinity preferences, other factors such as tidal regime become much more important in defining the use of mangroves.

6.4.1.4 Other factors

All other predictors were generally less important in defining the use of mangroves by these groups, which is likely related to the scale of analysis. Substratum and geomorphology was of some importance, with adult reef fish predictably found in rocky and sandy mangroves, and not in muddy mangroves, and all reef fish were positively associated with coastal rather than channelised mangrove locations (see Appendix C, Figures AC2, AC3 and AC4). It is difficult to distinguish to what extent these associations are driven by correlation with other predictors (Figure 6.7). Water depth was a consistently unimportant variable in all group models, however there were patterns in depth associations apparent for all groups but juvenile marine reef fish (see Appendix C, Figures AC1 to AC4). Similarly, while relative tidal height was not an important variable in any model, patterns were apparent in adult reef fish, where a positive relationship was observed between tidal height and mangrove use (see Appendix C, Figures AC1 to AC4). As is the case for salinity (outlined above), this lack of overall importance does not necessarily mean that these factors are unimportant in an absolute sense, as they nearly all contributed positively to model performance (see Figures 6.2, 6.3, and 6.5). The results of environmental vector fitting for inshore-user groups indicate that these prediction models were largely driven by the dichotomy between locations where reef fish were present, and locations where only coastal-estuarine species were present. This broad-scale view of mangrove habitat is likely to underrepresent drivers that, for instance, might be important to individual inshore-user groups within the restricted set of contexts in which they can be found in mangroves. The literature in which these other variables were found to be important (Table 6.2), suggests they could be drivers of mangrove use in some situations. At this scale however, the importance of the three variables outlined above (tide, distance to reef and salinity) dominated the prediction of the presence of inshore-user groups. Within the

broadly different contexts identified by this analysis (e.g. mangroves in small tidal ranges close to reefs, mangroves in low salinities far from reefs) other variables may be important predictors for particular groups. Defining where and when (under what contexts and conditions) these factors become important in determining the use of mangroves is an important task for future research.

6.4.2 Implications of context-dependence in mangrove use

The results of this study demonstrate that the role of mangroves can vary greatly from place to place. While there were some fish functional groups found in mangroves throughout their contextual range (see below), the vast majority of groups varied substantially. This implies that global, unified understandings of the function of mangroves is unachievable if it does not include context-dependence. The results of this study also demonstrate that mangrove function is largely predictable, based on context, and this has two major implications. Firstly, it implies that mangroves in similar contexts will share similarities in function, regardless of regional differences in species pools (e.g. Hemingson and Bellwood 2018). Therefore, a unified understanding of mangrove function may be possible within certain contexts. Secondly, it implies that broad differences in context between regions may result in broad differences in habitat function. Regional setting, such as tide, geomorphology and climate, interact to determine the range of different contexts present within a location. These large-scale system constraints could restrict the range of variability in habitat function, resulting in major differences between regions. In this way, paradigms about the role of mangroves as reef nursery grounds, which were developed and tested in the reef fringing mangroves of micro-tidal Caribbean and North America (Adams et al. 2006) ring true in this study in

similar contexts in the Indo-Pacific, but not in other contexts in the same biogeographic realm. The substantial variability in mangrove context throughout the Indo-Pacific is not found in the Caribbean, and therefore the use of mangroves by reef juveniles is a widespread, common occurrence, rather than a highly variable occurrence. Overall, contextual thresholds in the use of mangrove habitat provide clearer boundaries for safely extrapolating understanding of mangrove use among regions.

6.4.3 Variation in the ecological roles performed by *Rhizophora* mangroves.

How can we interpret and use the threshold values defined in this study? Current understandings of the nearshore environment hold that different habitat features are incorporated into ecosystems through complex mosaics of utilisation by fauna (Sheaves 2009). How habitat features, such as mangrove roots, are used by fauna depends on the kind of ecosystem they are incorporated into. Some aspects of environmental context appear to determine the kind of ecosystem mangrove roots are part of, in this case defined broadly as either coastal-estuarine or reef ecosystems, and constrain how fauna are able to utilise the mosaic of habitat features in their environment. The strong context-dependence found for different faunal groups indicates that it is possible to characterise the ecological role of mangrove habitats based on their environmental context. While the presence of fish does not necessarily demonstrate that a habitat has a particular function (e.g. as a nursery or foraging ground), fish presence is a necessary precondition to the performance of these functions. Therefore, these findings define boundaries within which these functions can occur, providing a basis on which to build an understanding of equivalence. Below, I use the

threshold values found in this study to generate testable hypotheses about the role of mangrove habitat in the nearshore environment based on context.

Where are mangrove roots part of reef ecosystems? Where mangroves occur close to reefs in microtidal regions, we can predict that they are part of reef ecosystems. Here, they are utilised by all reef fish groups. In the mangroves fringing the coast in these locations, we can expect to find both adults and juveniles of certain reef fish species, both those that are known to utilise brackish environments and those that solely inhabit marine waters. Here, it appears possible for mangroves to serve a nursery ground function for reef fish (sensu Adams et al. 2006, Igulu et al. 2014).

With increasing tidal range, mangroves tend to be less integrated into reef ecosystems, even when proximal to reef habitat. In macro-tidal regions where tidal amplitudes are generally below 3m, in mangroves close to reefs, we can predict that brackish tolerant reef juveniles, and occasionally marine reef juveniles and adult reef fish will be encountered (Barnes et al. 2012). In these locations, it is possible that mangroves serve as an important habitat in the juvenile phase of some brackish tolerant reef fish. Here, the way that reef fauna are able to use the mosaic of habitat features along the coast is constrained, as these fish would also have to use habitats other than mangroves at low tide (Krumme 2009).

Where are mangrove roots no longer part of reef ecosystems? In macro-tidal regions with tidal amplitudes generally greater than 3m, we can predict reef fish to be generally absent from the mangroves, regardless of proximity to reefs. As we move further from reefs, up till

about 1km we can still expect to find adult reef fish in the mangroves in micro-tidal regions, and in all regions where tidal amplitudes are generally below 3m, we can expect to encounter some brackish tolerant reef juveniles. At greater distances from reefs, reef fish become rare in this habitat, and apart from some species that are known to make extensive large-scale ontogenetic migrations, such as *Lutjanus argentimaculatus* (Russell and McDougall 2005), we can predict that mangroves no longer form an important part of reef ecosystems.

Where are mangrove roots part of coastal-estuarine ecosystems? When located in a brackish estuary, we can expect to consistently find coastal-estuarine fish in the mangroves, regardless of tidal regime. Here, the mangrove edge appears to provide important habitat for this group, where it may provide important feeding and refuge function (Blaber 2008, Nagelkerken et al. 2008). In marine waters far from reefs, we can expect to occasionally find coastal-estuarine fish, regardless of tidal regime.

How do different eco-functional groups use mangroves in these locations? In microtidal regions, when mangroves are close to reefs, we can predict assemblages to contain a diversity of eco-functional groups, including small herbivores, omnivores, and zoobenthivores that feed on sessile prey – groups that are rare in mangroves elsewhere. In macro-tidal regions with tidal amplitudes generally greater than 3m, we can predict the assemblage to be dominated by zoobenthivores that feed on mobile prey, and also contain other large bodied eco-functional groups. Here, small herbivores, small omnivores and small zoobenthivores that feed on sessile prey should be rare. In mangroves throughout the entire range of contexts sampled in this study, I can predict zoobenthivores that feed on mobile prey to be present,

and I can predict large bodied piscivores to be present. Given the substantial differences in the use of mangroves by coastal-estuarine and reef faunal groups, this is probably due to functional replacement – coastal-estuarine fish will fill these roles in some parts of the seascape, and reef fish will fill these roles in others. This suggests that mangroves consistently provide valuable habitat for both eco-functional groups. Perhaps mangroves throughout the contexts in this study consistently support mobile invertebrates and nektonic prey at densities that make them consistently valuable feeding grounds for these two trophic groups. The importance of mangroves as feeding grounds is known to vary considerably in different environmental contexts (Nagelkerken and Van Der Velde 2004a), but crabs and fish are relatively consistent features (Mattone 2016) and common prey items (Baker and Sheaves 2005, Lugendo et al. 2006). Perhaps, at least along the seaward edges of forests, access to mobile invertebrates and larger nektonic prey remains high, either inside the forests (Sheaves and Molony 2000) or proximal to them (Nagelkerken and Van der Velde 2004b), despite differences in environmental context.

Some substantial sections of important contextual space were not surveyed. In particular, in this study macro-tidal regions with extreme tidal amplitudes are represented by semi-arid North Western Australia, meaning that outside monsoonal flooding, most mangrove forests experience marine salinities. Therefore, from these results, I cannot make predictions about the role of mangroves in brackish waters under extreme macro-tidal amplitudes. There are locations in the Indo-Pacific that would be appropriate to test the role of mangroves under these conditions, such as the tropical Eastern Pacific coast of Central and South America, and studies from these regions clearly demonstrate that brackish mangroves here similarly provide important habitat for coastal-estuarine species (Castellanos-Galindo et al. 2013,

Castellanos-Galindo and Krumme 2015). Another important section of contextual space to examine is micro-tidal mangroves at large distances from reefs (e.g. >2km). Equivalent *Rhizophora* prop-root habitat did not occur in these contexts in our study sites, but there is likely to be equivalent habitat in Sumatra and Sri Lanka. It would be important to test whether distance to reef constrains the use of mangroves by reef fish – particularly adult reef fish – under these conditions. Overall, testing the model proposed above, and finding exceptions to these predictions, will be an important pathway to advance understanding by identifying other important aspects of variation in the ecological roles of this habitat.

6.4.4 Limitations:

As with any gear type, inherent limitations in the video survey method used in this study could restrict our view of mangrove habitat use. Due to low visibility during the monsoon season in most of the regions sampled, I could not incorporate comparable data on how fish use mangroves during this period. Likewise, I could not incorporate comparable data on nocturnal use. I surveyed the forest edge habitat, and so may miss any patterns related to penetration of the forest by fish. Cameras were placed on the substratum, and therefore in deeper locations, would not record fish using mangroves at the water surface. A few species have very specific forest use patterns, and appear to remain at the surface, or follow surface waters into the forest (Sheaves et al. 2016). Therefore, at higher tides in macro-tidal regions some species may be absent from edge samples for these reasons. Nevertheless, as the habitat (*Rhizophora* prop roots at the seaward edge of the forest) remained consistent between all locations, our results still demonstrate a significant divergence in habitat use, and hence a difference in function. Investigating the fine scale use of entire mangrove forests across a

range of different contexts will be required to understand the true context-dependence in the value of mangrove forests as a whole. Despite these limitations, these results provide compelling evidence that the role played by fringing *Rhizophora* roots in nearshore ecosystems is highly context dependent.

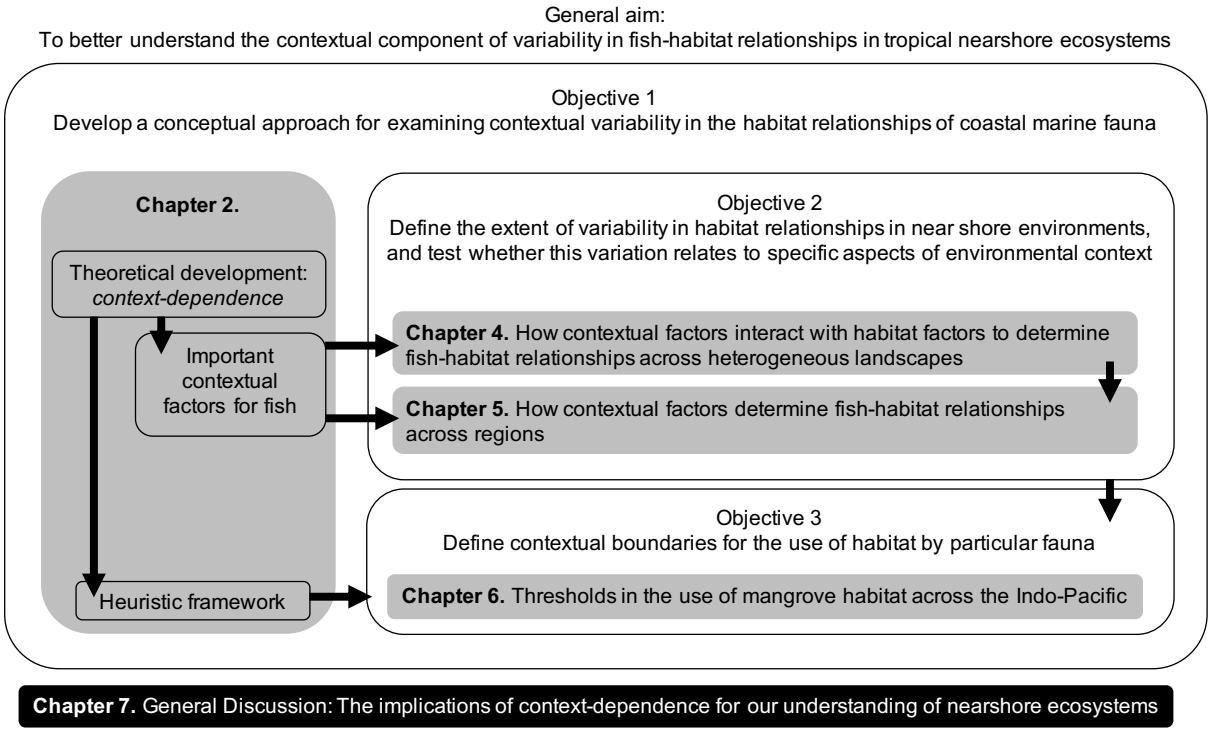
There are, of course, a variety of different types of mangroves. *Rhizophora* prop-roots are only one of a range of different structural forms under the broad category of 'mangrove habitat'. *Avicennia* and *Sonneratia* mangroves produce a very different kind of structured habitat composed of a 'field' of pneumatophore roots, and *Nypa* mangroves produce an innundated maze of trunks littered with fallen palm fronds. Fish are known to relate to these kinds of structures differently (Ronnback et al. 1999, Nagelkerken and Faunce 2008). Mangrove species differ in their distribution throughout the world and along environmental gradients (Duke et al. 1998). As a result, the structural form of mangrove habitat is likely to vary in different environmental contexts, such as within the intertidal zone, and across climatic and tidal regimes. How differences in the structural habitat characteristics of mangroves interact with environmental context to determine the value of mangroves to fish is likely to be highly complex. This remains to be explored, and is an important area for future research. However, the results of Chapter 5 suggest that tide, seascape and salinity strongly influence mangrove fish fauna either regardless of, or in concert with, mangrove type.

6.4.5 Wider implications:

A particular biogenic structure, in this case *Rhizophora* prop roots, was used by different sets of fauna under different environmental conditions. Because of this, our study suggests that the ecological roles played by certain habitat or vegetation types can be highly context dependent. Further, the factors of context that matter, and the specific boundaries of context-dependence appear to be unique for each specific ecological role. While this represents a first step in delineating contextual boundaries in the use of mangrove roots by fish, I hope that it can provide a basis on which to test predictions, and a blueprint for defining the context-dependence of the use of other habitat structures.

Developing, testing, re-building and re-orienting these models are essential tasks for ecologists, as they provide understanding of habitat function at scales relevant to environmental management. By integrating landscape factors with other environmental factors that determine habitat function, we can build a more robust understanding of the elements that lead to resilience of ecosystems, and how ecosystems might respond to environmental change and human intervention.

7 General Discussion



7.1 Key contributions

In the study of coastal systems, serious gaps exist as to the extent to which animal-habitat relationships from one location are transferable to another, what the limits are on our ability to generalise, and how to set those limits. Prior to the research presented in this thesis, our understanding of variability in fish-habitat relationships due to environmental context was generally limited to the action of particular factors in particular situations. How multiple factors influence habitat use over local and regional scales was largely unexplored, particularly in tropical coastal systems. While the large body of evidence required to address these fundamental gaps in coastal ecology has yet to mature, in this thesis I have developed a cohesive conceptual approach for integrating understanding across the multiple contextual factors at play in a particular location, and have tested this approach over a large geographic area, in an effort towards developing a global understanding that can reconcile differences between regions.

This research has revealed that context-dependence is a pervasive defining feature of fish habitat use in tropical coastal areas. Context-dependence in habitat use appears to be widespread; throughout the world, a wide range of different habitat relationships exhibit dependence on a range of different contextual factors (Chapter 2, Section 2.4). Context-dependence is apparent in the full suite of different habitat features available to fish (Chapter 4) and, at least in the wet-tropical region studied, context is a more important structuring force in habitat relationships than habitat features themselves, with an entirely different set of juvenile fish species using the same set of habitat types in directly adjacent estuarine and marine contexts (Chapter 4, Section 4.4). Across regions, context-dependence appears to

explain a large proportion of variability in the relationships between fish and mangroves (Chapter 5, Section 5.4), and predicts the use of mangroves by key functional groups (Chapter 6, Section 6.4).

Why is context-dependence such a pervasive feature of fish-habitat relationships? Context-dependence is essentially an artefact of the way ecologists deconstruct complex systems in order to gain predictive power. In coastal systems, habitat features, such as patches of vegetation of a particular type, are not islands unto themselves – they are part of the coastal ecosystem mosaic (Sheaves 2009), an interacting patchwork of different habitat features linked by the movement of organisms, productivity and nutrients (Nagelkerken 2009a). As outlined in Chapter 1 Section 1.1, models of habitat relationships are reductionist models of ecosystems. These models are often assumed to be transferable, or equivalent, between locations, because the habitat features used in these models are assumed to be incorporated into ecosystems that are more or less equivalent (Figure 7.1), or because the relevance of the broader ecosystem is disregarded entirely. These assumptions can be violated in two major ways. Firstly, similar habitat features may be incorporated into very different ecosystems, as was the case in Chapter 4. Here, although habitat types were similar between estuarine and marine contexts, they appeared to function as parts of very different seascape nursery mosaics. Secondly, similar habitat features may be parts of apparently similar ecosystems, but these ecosystems may not be equivalent in key functional ways. This appears to be the case in Chapter 6, where mangroves in locations very close to reefs – (i.e. part of back-reef lagoonal ecosystems) – still differ markedly in their use by reef fish due to tidal influence. Here, while these back-reef lagoonal systems appear outwardly similar, their key mechanics appear to be markedly different, resulting in the predictable use of mangroves in some

locations and not others (Chapter 6, Section 6.4.1.1). Context-dependence can be viewed as an artefact of the assumption that the various ecosystems in which a habitat feature occurs are functionally equivalent. In fact, they vary substantially, and this variation is pivotal in determining the function of a habitat feature for fauna. Examining context-dependence provides a useful vantage point from which to view ecosystems; important contextual factors are those that constrain aspects of ecosystem function relevant to the fauna under investigation.

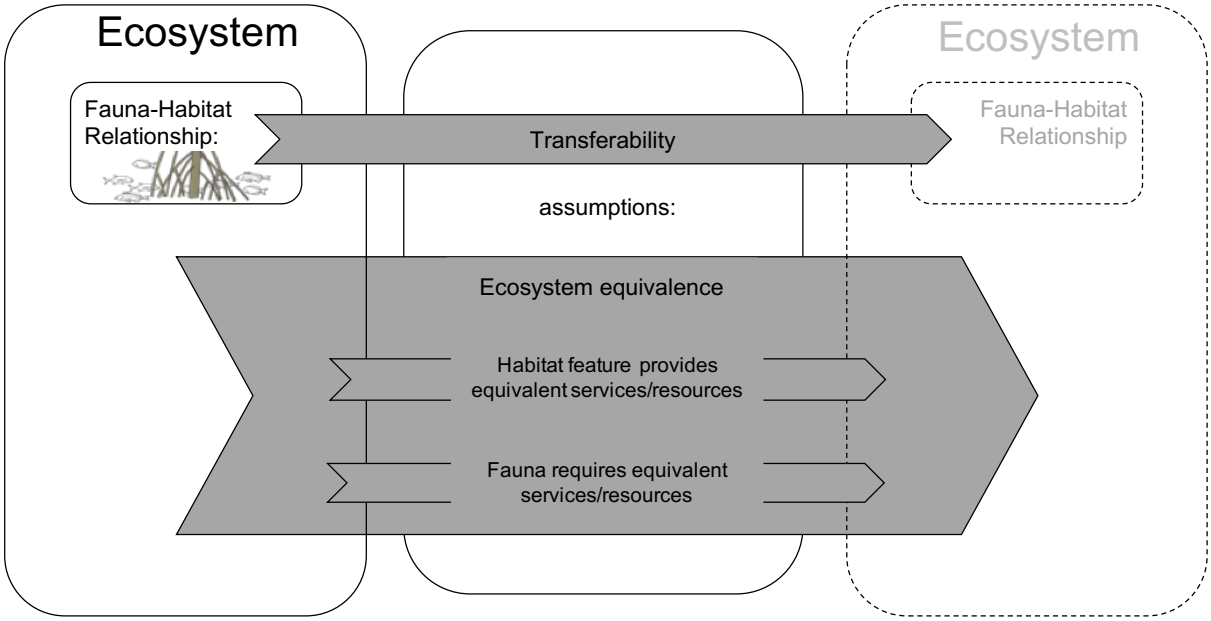


Figure 7.1 Conceptual diagram of the assumptions underlying the transfer of habitat-relationships from one location to another.

7.2 Key Implications

7.2.1 Non-equivalence of habitat relationships between different contexts

In the most basic sense, context-dependence in fish-habitat relationships implies that patches of the same habitat type may not fill the same ecological role for fish in different locations. This is distinct from the idea that habitat *quality* can vary between locations. Even though two habitat patches may be similar in a variety of measurable ways, they may function as quite different ecological entities. This implies that we cannot rely on measures of quality alone to determine function. Many contextual factors can vary over relatively small scales. Patches of the same habitat type can perform different roles for fish, based on where they are within single systems, such as within a single atoll, bay, estuary or river system. Variability occurs at larger scales, such as between systems and between regions. This questions the assumption that habitats provide the same services in different locations, and the parallel assumption that fish will relate to, and require, the same habitat type in different locations (Figure 7.1). Additionally, if relationships are potentially aliased between locations (see Chapter 2, Section 2.2), this calls into question assumptions of equivalence in the nature and consequences of those relationships, such as how a species will respond to landscape level change.

Context-dependence complicates and constrains the ways it is reasonable to interpret fish-habitat relationships. It implies that by following typical conventions used in the past to interpret the results of field studies, we risk generating erroneous scientific understanding.

Often, findings are understood in the light of paradigms – often global paradigms – that are used to connect observed responses with ecological mechanisms and processes (Sheaves et al. in review). This is common practise in ecology, and results in the construction of paradigms underpinned by the usually untested assumption that ecosystems are equivalent in different contexts (Sheaves 2012). In coastal ecology, there is an interlinked set of paradigms that relate fauna-habitat relationships to ecological outcomes, centring on connectivity. The nursery paradigm links habitat use throughout ontogeny with population persistence. The nursery paradigm holds that particular juvenile habitats contribute disproportionately to spatially separated adult populations of particular faunal species, and thus the presence, health and integrity of these juvenile habitats is linked to overall population maintenance and resilience (Beck et al. 2001, Nagelkerken 2009b). Paradigms around nearshore ecosystem connectivity link habitat use over multiple scales with local and offshore productivity. The habitat use patterns of fauna during ontogeny, over seasonal cycles and during daily foraging and refuge forays, link nearshore habitats through the movement of productivity, such that impacts and disturbances in nearshore habitats correspond to changes in local and offshore productivity (Nixon 1980, Deegan 1993, Bouillon and Connolly 2009). Paradigms around fisheries habitat fuse these concepts, linking habitat use with local and offshore fish catch, through nursery ground concepts (Blaber 2009). Ecosystem services paradigms link these habitats directly with the economic value of fisheries (Barbier 2000, Barbier et al. 2008). The deductive causal links in these paradigms are often based on combining understanding from various contexts. For example, the correlations between coastal fisheries and mangrove forest extent in Northern Australia was attributed to the use of the forest area by juveniles of fisheries species (Manson et al. 2005) in light of global studies. However, recent studies from that region have found most fisheries species make limited use of the forest area, and typically use either the perimeter only (Sheaves et al. 2016) or other estuarine habitats

(Bradley et al. 2017). In this case, the response of fisheries production to mangrove forest extent in different parts of the world are likely aliased – in some cases driven by the use of mangrove forests and in others potentially driven instead by the system level value of the forests (Sheaves et al. 2015). In this example, the degradation of mangrove forests will likely have very different impacts on fisheries depending on the kind of habitat relationships links that exist between mangroves and fish. This considerable source of potential variability needs to be understood if we are to assess the value of different habitat types to fish (e.g. Whitfield 2017), and use these assessments to make management decisions (e.g. Rosenberg et al. 2000). If not, we risk generating and perpetuating false information, with serious consequences for the management of ecosystems (Sheaves et al. in review).

The tacit assumption of equivalence in habitat relationships between locations is also pervasive in the application of scientific understanding for management purposes. Context-dependence complicates assumptions of equivalence in the value of a habitat for fauna, how that value is derived, and the response of fauna to changes in habitat. Wherever they are employed, if assumptions of equivalence are violated, there are likely to be serious consequences. For habitat-based conservation actions, this could lead to targeting incorrect habitat for the protection of a species, leaving critical habitats unprotected (McAlpine et al. 2008). Assumptions of equivalence lie at the heart of the concept of environmental offsetting, where the degradation or destruction of habitat in one location is compensated for by the protection, restoration or creation of similar habitat elsewhere, with the goal of 'no net loss' in ecosystem values and functions (Robertson 2000, Middle and Middle 2010). While authors have called for strict caveats around this concept, to ensure that offset actions actually result in the maintenance of functional values (often the maintenance of faunal populations), it is

believed that ‘no net loss’ can be achieved if the habitat features (such as vegetation) are simple enough that they can be adequately replicated elsewhere (Gibbons and Lindenmayer 2007). Offset locations are often far from impact locations (Robertson 2000). If these functional values are context-dependent, this practise could still lead to the degradation of critical habitat functions, even when a net balance in high quality habitat area is achieved. Similarly, assumptions of equivalence in habitat function can form the basis for restoration activities in general, and for judging the success of interventions. Often, a detailed understanding of the functional values of a site targeted for restoration prior to degradation is lacking, especially when degradation has occurred over long time frames. Even when available, this historical information may not provide an adequate reference for the functional values of a site under present environmental conditions. Hence, similar habitat in other locations are often chosen as reference sites (Choi 2004). Again, if these functional values are context-dependent, high quality habitat may be successfully restored, but assumed habitat functions may not return simply because they are based on knowledge from a different location. In all of these applications, failure to deliver expected functional values can have serious social consequences (Rose et al. 2015). Thus, societies may erode their natural capital while labouring under the misapprehension that they are maintaining it.

7.2.2 Equivalence of habitat relationships in similar contexts

Context-dependence in fish-habitat relationships also implies that certain environmental drivers define ecosystem function to such an extent that they can predict relationships between key components in those ecosystems, namely motile fauna and fixed biogenic features. In Chapter 4, marine and estuarine contexts defined the species that use submerged

aquatic vegetation, mangrove forests and rocky reefs throughout a region, while in Chapters 5 and 6, tide, seascape and marine-estuarine context defined the families and functional groups that used mangrove habitat throughout the Indo-Pacific. These relationships were predictable, which implies that, while we may not be able to generalise our understanding of habitat relationships universally, we are able to set meaningful, quantifiable limits on our understanding of particular nearshore habitat relationships. This means that the problem of generalisation is at least partially tractable – for some relationships, real transferability (sensu Wenger and Olden 2012) should be possible with a robust and sufficient understanding of context, by validating the assumptions that underlie transferability (Figure 7.1). With structured and directed research effort into the context-dependence of particular relationships, our ability to make correct predictions will likely increase.

Equivalent environmental contexts forge equivalent coastal ecosystems (sensu Sheaves 2012) in which paradigms linking habitat relationships with nearshore ecosystem function make coherent sense. It is clear from the research presented in this thesis along with a growing number of studies and reviews (Igulu et al. 2014, Litvin et al. 2018), that variation in certain contextual factors must be considered when discussing ecosystem functions. How do these forces create ecosystems that are equivalent in important ways? Connectivity within ecosystems is determined by physical and ecological conditions, spatial structure and temporal patterning, and it is connectivity that defines the value of nearshore systems for nekton, how that value is derived, and how it is linked with productivity, resilience and economic value (Sheaves 2009, Litvin et al. 2018). This is apparent for the contextual factors examined in this thesis.

Broad equivalence in seascape structure will result in broad equivalence in key aspects of ecosystem functioning. Where multiple habitats like coral reef, seagrass, mangroves and macroalgae occur in mosaics of adjacent patches, nekton can move between them to satisfy their requirements on a daily basis (Lugendo et al. 2006, Dorenbosch et al. 2007, Nagelkerken 2007). This promotes connectivity between habitats. Ecosystem functions of interest, such as fish production, are emergent properties of these mosaics (Sheaves et al. 2015). Where these habitat types exist in isolation, fauna persist without these complex inter-habitat connectives (Nagelkerken et al. 2008, McMahon et al. 2012), and ecosystem functions such as fish production will be more directly the result of food-webs and processes occurring within the habitat.

Another broad difference in coastal ecosystem function is the divide between estuarine contexts and marine contexts. Physiological tolerances drive a natural divide between two broadly different faunas – one intolerant to low salinity and high turbidity, and the other tolerant to large fluctuations in both (Woodland et al. 2012, Whitfield and Pattrick 2015). Between these two faunas, differences in species specific life history strategies, which determine how seascapes are used by nekton (Potter et al. 2015), could alone produce widely different connectives, resulting in consistently different ecosystem functioning. Additionally, the different environmental conditions between estuarine and marine contexts also drive outcomes of ecosystem productivity (Lankford and Targett 1994, Koenig et al. 2007).

Finally, ecosystem connectivity is also modified by the tides. Significant tidal action forces nekton that use coastal habitats to perform tidal migrations (Lugendo et al. 2007a), connecting different parts of the seascape (Sheaves 2009). Where there is a lack of tides, connectivity is restricted to active animal movements, usually timed with the day-night cycle (Nagelkerken et al. 2000b, Krumme 2009). These two different regimes are likely to result in

consistent and predictable differences in ecosystem functioning (Krumme 2009), such as differences in the mechanisms that connect habitats with the export of juveniles to adult populations, i.e. nursery ground functioning (Sheaves et al. 2015, Litvin et al. 2018). This (Sheaves et al. 2015) could involve consistent differences in the degree of separation between predators and juvenile prey (Faunce and Layman 2009, Minello et al. 2012, Baker et al. 2015) and the importance of inter-habitat subsidies in support of juvenile growth (Igulu et al. 2013). Particular contextual differences result in broadly different types of ecosystem functioning, and it is crucial that paradigms linking habitat use to ecosystem resilience and productivity, and hence fisheries and economic value, are developed within the boundaries of equivalent ecosystem types.

There has been a general progression in the literature towards the incorporation of context into the construction of paradigms and theoretical development around the role of habitats in nearshore ecosystem function, in an attempt to ensure that general understandings are developed in robust ways. The long-standing approach of examining the nursery function of different 'habitat types' (e.g. Robertson and Duke 1987) has meant that the relationships under discussion (as they were defined) were highly vulnerable to context-dependence (as discussed in Chapter 2, Section 2.3). This conceptualisation of fish and decapod nurseries as single homogeneous habitat types is entrenched in the definition of nurseries that was widely adopted (Beck et al. 2001, Dahlgren et al. 2006). To limit paradigm construction to particular eco-physical contexts, a variety of refinements and qualifiers of the habitat type under discussion were employed. In the case of investigations of the nursery role of mangroves for reef fish, this was variously "clear water mangroves" (e.g. Barnes et al. 2012) and "non-estuarine mangroves" (e.g. Nagelkerken 2007). In a similar practise, some authors have

limited their development of theory around mangrove nursery function with the highly specific geomorphological qualifier of "back-reef" or "lagoonal" systems (e.g. Adams et al. 2006), which works to pin-point both physical (i.e. high salinity and low turbidity), and spatial (i.e. short distance to reef habitats) contexts. My findings indicate that this distinction between marine and estuarine contexts in the discussion of nursery function would be necessary for any structural habitat type in the nearshore environment (Chapter 4). In a similar way, authors have often limited paradigms around coastal nursery function to either the Caribbean or Indo-Pacific, due to the broad disagreement between those regions (e.g. Nagelkerken 2009b). This was usually a quasi-contextual limitation, a conscious response to substantial differences in ecosystem function thought to be due to tidal forces (e.g. Barnes et al. 2012). These distinctions made between different 'kinds' of mangrove habitat foreshadow the need for context explicit conceptualisations of coastal ecosystem function. Both of these somewhat vague limits around nursery function labour under untested assumptions of ecosystem equivalence. To what extent are all clear-water, non-estuarine or back-reef mangroves equivalent? Is a broad understanding of the nursery function of mangroves really possible across the Indo-pacific, or even the Caribbean, given substantial variation in tidal range and rainfall? My findings, and those of others (Kimirei et al. 2013), demonstrate important exceptions. There is a clear need for the development of context specific paradigms around nearshore ecosystem function, so that theoretical development can continue within explicit limitations.

Recently, the weight of evidence around spatially explicit nearshore habitat use by fish has led to a reconceptualization of nursery ground function. Syntheses of this emerging new paradigm have focused on connectivity, how and why it is maintained, and its central role in

determining nursery value (Sheaves et al. 2015, Litvin et al. 2018). In this new conceptualisation, nursery grounds are structures composed of hotspots in animal densities, mosaics of habitat used during daily cycles, flows of processes supporting the utilisation of these mosaics, and the pathways between areas used at different stages of ontogeny (Nagelkerken et al. 2015). This carries with it the fundamental underlying implication that nursery value is an emergent, location-specific phenomenon, and that understandings of nursery ground function must be context specific in order to capture the particular connections, and modes of connection that matter. For instance, a very different set of forces and connections are important in a clear-water, micro-tidal Caribbean nursery ground to a turbid, mesotidal salt marsh nursery ground (Nagelkerken et al. 2015). This has far-reaching implications for interlinked paradigms around coastal habitat productivity and fisheries value. Ideas that link fish populations and fisheries value to particular habitats through nursery contribution on a per unit area basis (Barbier 2000, Beck et al. 2001) need to be reinterpreted in the light of models where animal hotspots and migration corridors are key features, and where contribution depends on local conditions. Theories of nursery function and ecosystem service provisioning that are specific to particular contexts would clearly be better positioned to capture the nuances of the mechanisms involved in different situations. Given that coastal zones vary in multifaceted and complex ways throughout the world, ecosystem function will be somewhat unique in every location. However, understanding context-dependence in key ecosystem processes, including habitat use (such as in this thesis), daily movement patterns, ontogenetic migrations, spatial subsidies and trophic relays, could guide the best ways to draw these important paradigmatic boundaries, thus carving the world at its natural joints (sensu Plato 1914).

To understand how the context-dependence in fauna-habitat relationships observed in this thesis might indicate a wider context-dependence in nearshore ecosystem functioning, further extensive research is required within the framework described in Chapter 2 (Section 2.5).

An important avenue of enquiry is to understand whether there is context-dependence in other components of nearshore ecosystems beyond those examined in this thesis. Freshwater fishes are a key component in the fauna of many large mangrove dominated systems, along with coastal and estuarine groups, whereas reef fishes are largely absent. The relationship between coastal and estuarine habitats and the freshwater component of the assemblage may vary according to context, perhaps, like reef fishes, driven by rainfall and tidal forces that regulate access and salinity regimes (e.g. Garcia et al. 2003). These relationships are yet to be quantified, particularly in the case of the use of marine and estuarine nurseries by amphidromous fishes (Maeda and Tachihara 2014). These kinds of systems are dominant in south east Asia (e.g. Borneo), eastern South America (e.g. Amazon and Orinoco deltas), and west Africa, and context-dependence in the functional role of different habitats would allow of a better understanding of ecosystem function.

The nocturnal use of habitats is another component of nearshore ecosystems where data is lacking, but context-dependence may be important. The great majority of our understanding of habitat use comes from models of daytime patterns, but the nocturnal use of habitats by fish tend to be quite different (Nagelkerken et al. 2000b, Hagan and Able 2008). Some fishes, such as some members of Heamulidae and Lutjanidae, tend to utilise feeding habitats at night (Rooker and Dennis 1991, Nagelkerken et al. 2000b). These types of relationships are critical to ecosystem function, but also exhibit variability which may be due to context-dependence

(Hammerschlag et al. 2010). Similarly, we lack data on habitat relationships in highly turbid areas, where habitat relationships are likely to be different (Jude and Pappas 1992, Miner and Stein 1996). The video methods that allowed for comparisons across diverse ecosystems and habitat types in this thesis are not feasible at night time or in turbid areas, therefore the challenge remains to develop techniques to determine broad patterns of fish-habitat relationships under these conditions.

A deeper understanding of context-dependence in habitat use is also required. While my research examined patterns of animal presence, information is needed on the contextual variability in how fauna use particular habitats as refuge or feeding sites (Kimirei et al. 2015), and the effect this has on key ecosystem processes like herbivory, predation and trophic relay. This could be obtained by examining gut content and stable isotope values of key species (Nagelkerken and Van der Velde 2004b, Lugendo et al. 2006), and combining this information with field experiments such as algal assays and tethering trials (e.g. Martin et al. 2018). Finally, while it is assumed that context-dependence in the use of particular habitat types is driven by substantial differences in seascape use, this must be empirically established. Are patterns of inter-habitat movement by animals, either on a fine scale or throughout ontogeny, in some way predictable based on context? Comparing the otolith micro-chemistry of key species across contexts allows for a broad understanding of context-dependence in coarse movement patterns. In this thesis, comparisons of broad movement patterns were carried out for *Lutjanus argentimacultus* and *Lutjanus johnii* in Appendix D, and are discussed therein. When combined with acoustic telemetry and visual census studies targeted at particular contexts, a finer scale understanding could validate any observed patterns (as demonstrated in Appendix D). Gathering this evidence for multiple taxa on a

large scale would be a substantial undertaking, but is possible with existing technology, and may substantially improve current understandings of nearshore ecosystems.

7.3 Application

The robust understanding of context-dependence described above could provide critical information for on-ground management of nearshore systems, by ensuring that management decisions are based on robust and relevant knowledge, rather than poorly-supported paradigmatic understanding. There is a vital need for the translation of ecological knowledge into the kind of information that is required for management, i.e. information that is specific to the scale and context of a particular management problem (Schlesinger 2010, Beier et al. 2017, Enquist et al. 2017). This kind of knowledge is required to ensure that restoration actions are effective and appropriate (Palmer and Filoso 2009, Rose et al. 2015), and is also critical for effective spatial planning. For example, the link between mangrove proximity and the persistence of functionally and economically important reef fish (e.g. Nagelkerken et al. 2017), indicates the importance of incorporating mangrove-reef connectivity into marine reserve design, to enhance reserve performance (Olds et al. 2013, Olds et al. 2014). However, the results of Chapter 6 indicate that relationships between reef fish and mangroves appear to break down in large tidal range contexts, so this may not be an appropriate way to approach marine reserve design throughout the Indo-Pacific. Environmental management decisions almost invariably rely on knowledge that is based on information from other places. For practitioners, knowing when you are working inside the limits of available knowledge, and knowing when you are in situations beyond those limits, is critical in weighing up potential actions and their outcomes. In this way, a well-developed understanding of context-

dependence would provide an effective means to translate scientific understanding into actionable knowledge for management.

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Appendix A: Supplementary materials for Chapter 4

Supplementary methods – survey design

Some biota and substratum combinations appear to be highly represented in my data set (n>100). These habitats were present across the entire depth range (0.5 – 10m) in my study zone. To capture any differences in juvenile habitat use related to depth, sufficient replication over the depth range was required. Some biota and substratum combinations are poorly represented in my data set (n < 15). These habitats were rarely encountered and could not be located during targeted sampling. While as a distinct combination of biota and substratum their replication may be too low to adequately characterise them as a unique habitat, they form part of the broad replication of each biotic category or substratum category. For instance, 'woody debris – boulder' forms part of the range of variability present in all boulder samples, or all woody debris samples, and allows for the full range of habitat encountered in my study zone to be accounted for, avoiding *a priori* exclusion of samples. Further sampling would be required to understand their role as distinct habitat.

Table AA1. Of the 20 different biota and substratum combinations found in the Hinchinbrook region, 18 were found in estuarine contexts and 10 were found in marine contexts. Categories are shown in the format (*dominant biota*) - (*substratum texture*). The number of samples in my dataset is shown for each context, and each habitat type within each context. SI = sessile invertebrates

Context and habitat type	Count of samples
estuarine context	1074
bare - boulder	119
bare - cobble	33
bare - gravel	56
bare - mud	335
bare - sand	209
SI - boulder	52
SI - cobble	16
SI - mud	8
macroalgae - cobble	9
mangrove - cobble	4
mangrove - mud	57
mangrove - sand	35
seagrass - cobble	3
seagrass - mud	56
seagrass - sand	2
woody debris - boulder	4
woody debris - cobble	9
woody debris - mud	34
woody debris - sand	33
marine context	241
bare - boulder	19
bare - cobble	19
bare - sand	24
macroalgae - cobble	6
macroalgae - sand	28
mangrove - cobble	11
mangrove - sand	37
seagrass - sand	36
coral - solid	61
Grand Total	1315

Table AA2. Frequency of occurrence of juvenile fish observed in video sampling of coastal habitats. Numbers indicate how many samples a particular taxonomic/life stage group occurred in each habitat, divided by the total number of samples recorded in each habitat, presented as a percentage (rounded to whole numbers). Taxa presented are all those observed in video samples of non-coral habitats. Habitats presented are the six defined by the mvCART (Fig. 3a), as well as shallow and deep coral, and those identified as a low-value habitat in Fig. 2 but presented separately here for comparison of assemblage structure – namely estuarine seagrass, estuarine open bottom habitat and marine open bottom habitat. The table has been constructed to facilitate comparisons between habitat types, grouped within black borders, and contexts, identified by shading. Dark shading indicates habitat from estuarine areas, light shading indicates habitat from marine areas. JP = (entire) Juvenile Phase, EJP = Early Juvenile Phase, LJP = Late Juvenile Phase.

	Estuarine mangroves and woody debris	Marine mangroves	Estuarine seagrass	Marine seagrass and macroalgae	Estuarine rocky reef, shallow	Estuarine rocky reef, deep	Marine rocky reef	Coral, shallow	Coral, deep	Estuarine open bottom habitat	Marine open bottom habitat
TOTAL SAMPLES:	176	37	58	70	71	169	49	29	32	600	24
Acanthuridae											
Acanthurus auranticavus JP	0	0	0	1	0	0	4	0	0	0	0
Carangidae											
Caranx sexfasciatus JP	1	16	0	0	0	1	4	0	0	0	0
Chaetodontidae											
Chaetodon JP	0	0	0	6	0	0	6	14	0	0	0
Labridae											
Labridae JP	2	3	0	49	37	54	4	34	22	1	0
Choerodon anchorago EJP	0	0	0	6	0	0	0	0	0	0	0
Halichoeres nigrescens JP	2	0	0	0	37	54	0	0	0	1	0
Hemigymnus melapterus JP	0	0	0	0	0	0	2	21	13	0	0
Stethojulis strigneverJP	0	0	0	50	0	0	2	0	0	0	0

Scarinae											
Scarine EJP	0	0	0	40	0	0	0	10	3	0	0
Scarine LJP	0	0	0	21	0	0	0	7	13	0	0
Leptoscarus vaigiensis EJP	0	0	0	7	0	0	0	0	0	0	0
Scarus rivulatus LJP	0	0	0	21	0	0	0	0	0	0	0
Scarus flavipectoralis LJP	0	0	0	0	0	0	0	3	6	0	0
Lethrinidae											
Lethrinus EJP	4	3	22	76	4	3	4	0	0	0	4
Lethrinus LJP	1	24	0	37	3	2	14	0	3	0	0
Lethrinus atkinsoni EJP	0	0	0	6	0	0	0	0	0	0	0
Lethrinus atkinsoni LJP	0	0	0	3	0	0	0	0	0	0	0
Lethrinus genivittatus EJP	0	0	0	13	0	0	0	0	0	0	0
Lethrinus genivittatus LJP	0	0	0	6	0	0	0	0	0	0	0
Lethrinus harak EJP	0	0	0	6	0	0	0	0	0	0	0
Lethrinus harak LJP	0	11	0	30	0	0	12	0	0	0	0
Lethrinus nebulosus EJP	0	0	0	1	0	0	0	0	0	0	0
Lethrinus obsoletus EJP	0	0	0	3	0	0	0	0	0	0	0
Lethrinus obsoletus LJP	0	0	0	26	0	0	2	0	3	0	0
Lethrinus virgatus EJP	0	0	0	1	0	0	0	0	0	0	0
Lutjanidae											
Lutjanus argentimaculatus EJP	6	0	0	0	3	0	0	0	0	0	0
Lutjanus argentimaculatus LJP	24	0	0	0	18	3	0	0	0	1	0
Lutjanus carponotatus EJP	0	0	0	36	0	0	4	10	3	0	0
Lutjanus carponotatus LJP	0	3	0	7	0	0	10	3	3	0	0
Lutjanus fulvus LJP	0	0	0	0	5	2	0	0	0	0	0
Lutjanus fulviflamma EJP	15	70	0	31	14	2	4	0	0	1	46
Lutjanus fulviflamma LJP	0	16	0	1	1	1	0	0	0	0	0
Lutjanus johnii LJP	0	0	0	0	3	4	0	0	0	0	0
Lutjanus lemniscatus EJP	0	0	0	0	0	1	0	0	0	0	0
Lutjanus russellii EJP	12	0	0	0	30	16	0	0	0	0	0
Lutjanus russellii LJP	16	0	0	0	14	24	0	0	0	0	0
Mullidae											
Parupeneus barberinus EJP	0	0	0	3	0	0	0	0	0	0	0
Parupeneus ciliata JP	0	0	0	0	0	0	4	0	0	0	0
Parupeneus indicus EJP	0	0	0	6	0	0	0	0	0	0	4
Parupeneus spilurus EJP	0	0	0	1	0	0	0	0	0	0	0
Upeneus tragula EJP	0	0	0	16	0	0	0	0	0	0	0
Nemipteridae											
Nemipterid JP	1	0	0	11	0	4	20	14	16	0	0
Pentapodus paradiseus EJP	0	0	0	3	0	0	0	0	0	0	0
Scolopsis affinis EJP	0	0	0	1	0	0	0	0	3	0	0
Scolopsis bilineata EJP	0	0	0	1	0	0	0	3	3	0	0
Scolopsis lineata EJP	0	0	0	4	0	0	16	10	0	0	0

Scolopsis margaritifera JP	0	0	0	0	0	0	4	0	13	0	0
Scolopsis monogramma JP	0	0	0	3	0	0	0	0	0	0	0
Pomacentridae											
Pomacentrus JP	0	3	0	70	0	0	73	76	28	0	13
Pomacentrus tripunctatus JP	0	3	0	64	0	0	63	52	0	0	13
Pomacentrus spp. JP	0	0	0	26	0	0	29	55	28	0	0
Serranidae											
Epinephelus JP	0	0	0	4	0	0	0	3	3	0	0
Siganidae											
Siganus EJP	2	30	10	90	0	3	24	17	0	0	4
Siganus doliatus EJP	0	0	0	43	0	0	0	0	0	0	0
Siganus fuscescens EJP	0	3	10	66	0	3	6	3	0	0	0
Siganus javus EJP	2	0	0	0	0	0	0	0	0	0	0
Siganus lineatus EJP	0	3	0	10	0	0	0	0	0	0	0
Siganus spinus EJP	0	0	0	69	0	0	18	14	0	0	0
Sparidae											
Acanthopagrus JP	20	0	0	0	3	1	0	0	0	0	0
Sphyraenidae											
Sphyraene barracuda JP	0	3	0	0	0	0	0	0	0	0	0
Terapontidae											
Pelates quadrilineatus JP	0	0	10	36	0	0	0	0	0	0	0
Terapon jarbua JP	0	0	0	0	0	0	0	0	0	0	0
Terapon puta JP	0	0	2	0	0	0	0	0	0	0	0
Terapon theraps JP	0	0	7	0	0	0	0	0	0	0	0

Appendix B: Supplementary materials for Chapter 5

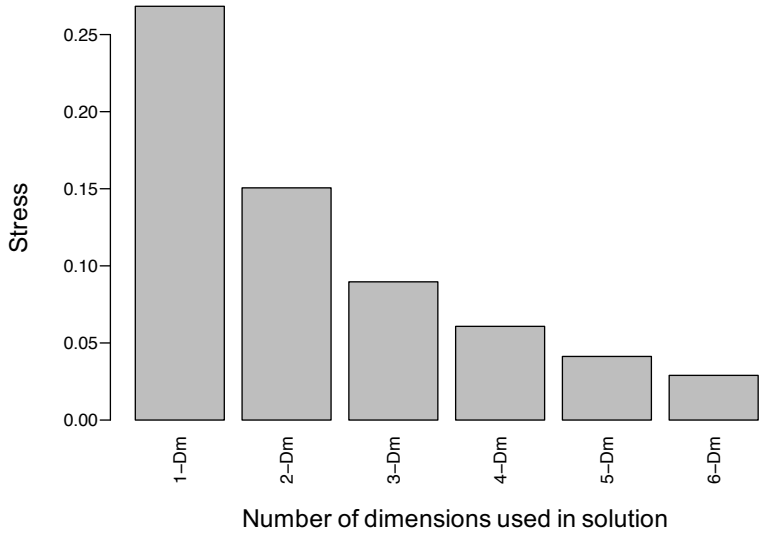


Figure AB1. Stress vs dimensions for the conventional data treatment, where only species with >10% occurrence across the entire dataset were included. Bars show the stress of multidimensional scaling solutions with increasing numbers of dimensions. A stress value below 0.2 indicates a reliable arrangement of points that is representative of the distance matrix used.

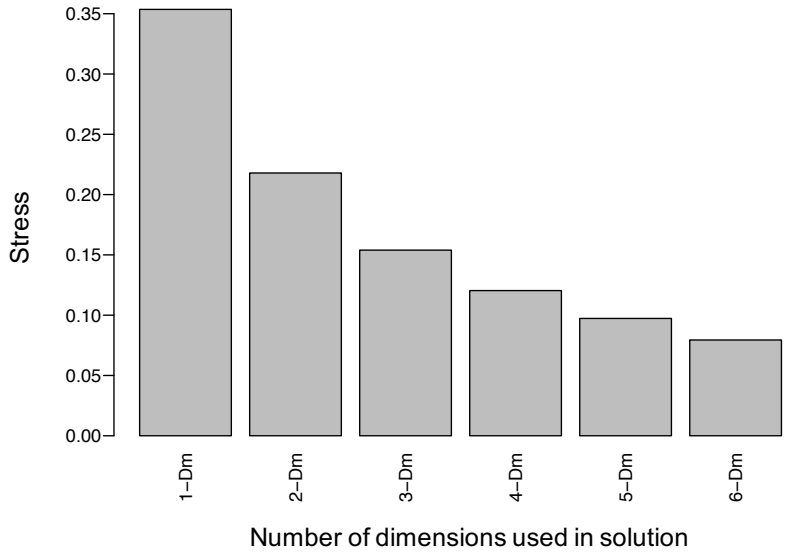


Figure AB2. Stress vs dimensions for the inclusive data treatment, where species with >10% occurrence in any region were included. Bars show the stress of multidimensional scaling solutions with increasing numbers of dimensions. A stress value below 0.2 indicates a reliable arrangement of points that is representative of the distance matrix used.

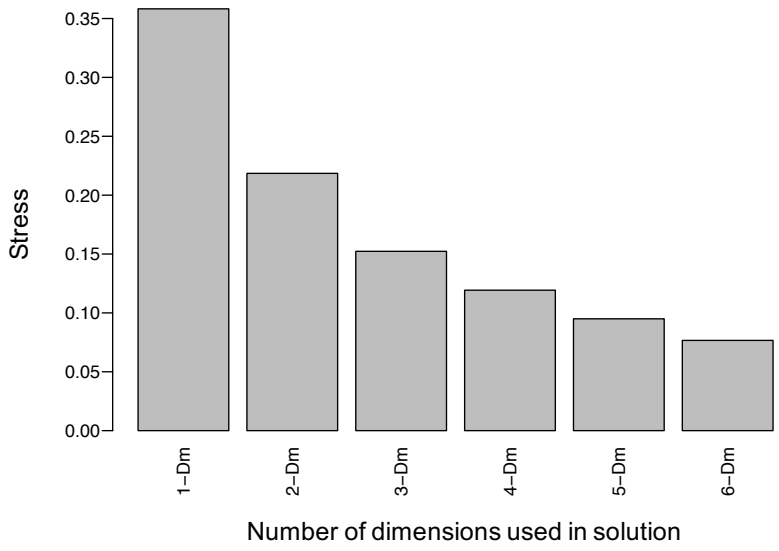


Figure AB3. Stress vs dimensions for the inclusive data treatment, where species with >10% occurrence in any region were included, excluding outliers. Bars show the stress of multidimensional scaling solutions with increasing numbers of dimensions. A stress value below 0.2 indicates a reliable arrangement of points that is representative of the distance matrix used.

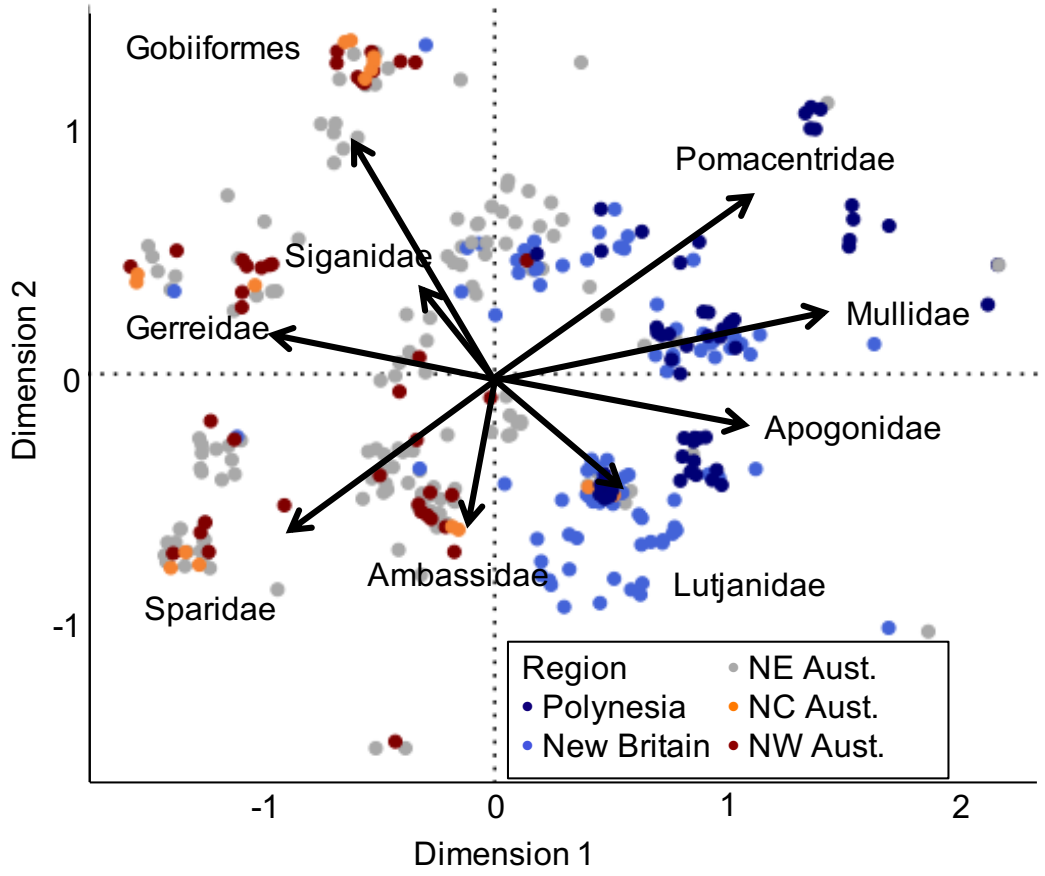


Figure AB4. MDS ordination displaying a 2D solution (stress: 0.149) capturing the differences between samples based on a conventional treatment of family level taxonomic assemblage composition. Dimensional values are scaled such that a distance of one unit represents a halving of assemblage similarity between samples. Taxonomic vectors represent the direction of positive correlation with the ordination space**.** Vector terminal position represents the location of highest occurrence in the space, calculated using the weighted average of sample abundances. Only taxa with a large (>0.5) distance from the centre of the ordination space (i.e. taxa that differ strongly across the ordination space) are shown. Points have been jittered (at a scale of 0.1 on each dimensional axis) to reveal quantities of points occurring at identical positions in the ordination.

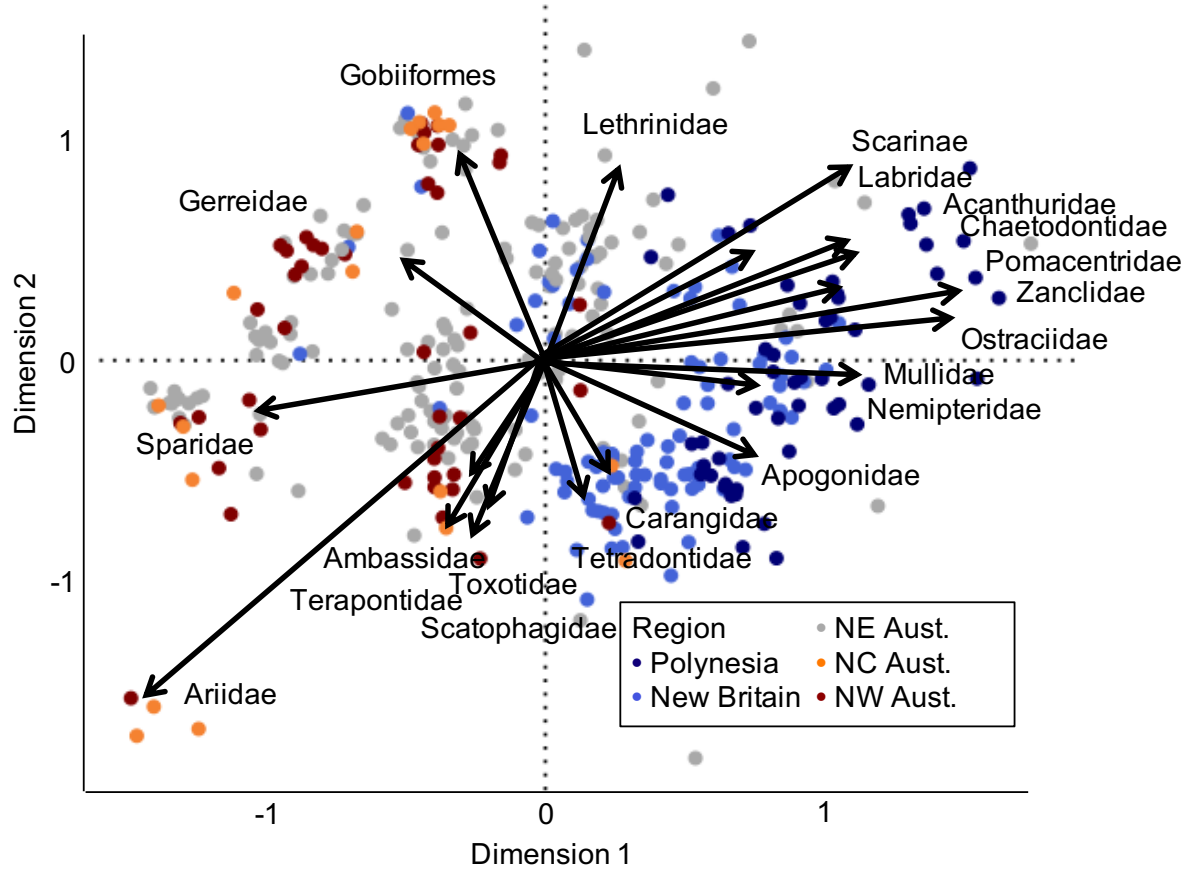


Figure AB5. MDS ordination displaying the first two dimensions of a 3D solution (stress: 0.153) capturing the differences between samples based on an inclusive treatment of family level taxonomic assemblage composition. Dimensional values are scaled such that a distance of one unit represents a halving of assemblage similarity between samples. Taxonomic vectors represent the direction of positive correlation with the ordination space**.** Vector terminal position represents the location of highest occurrence in the space, calculated using the weighted average of sample abundances. Only taxa with a large (>0.5) distance from the centre of the ordination space (i.e. taxa that differ strongly across the ordination space) are shown. Points have been jittered (at a scale of 0.1 on each dimensional axis) to reveal quantities of points occurring at identical positions in the ordination.

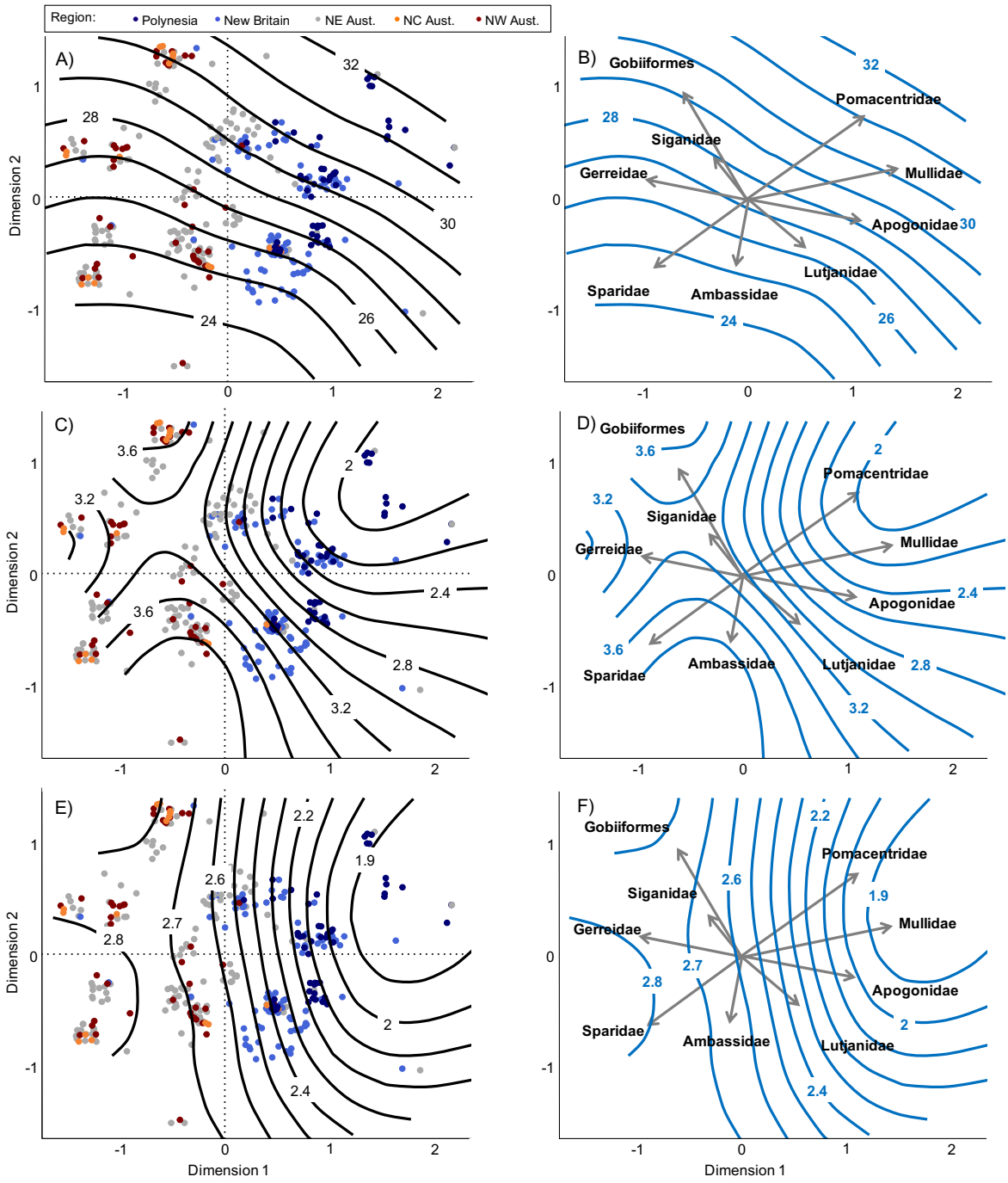


Figure AB6. Results of surface fitting on the ordination produced using a conventional data treatment, where only taxa present in >10% of samples were included. Top panels show the fitted surface for salinity, which explained 9.1% of variation between points. Middle panels show the fitted surface for distance to reef, which explained 42% of variation between points. Bottom panels show the fitted surface for tidal amplitude, which explained 61% of variation between points. Left panels show surfaces with sample points for reference, Right panels shows surfaces with species vectors for reference.

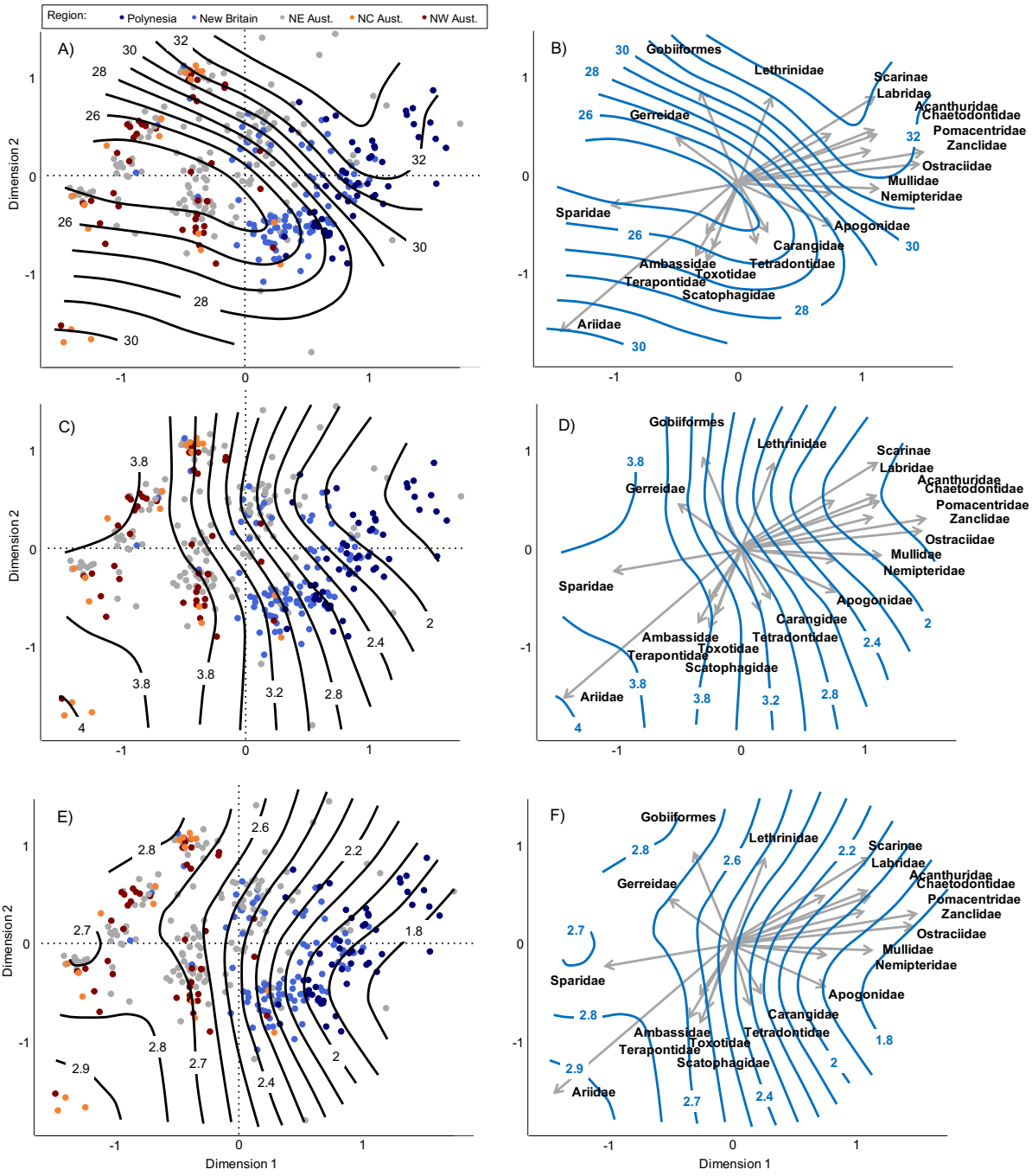


Figure AB7. Results of surface fitting on the ordination based on an inclusive treatment of family level taxonomic assemblage composition. Top panels show the fitted surface for salinity, which explained 14.5% of variation between points. Middle panels show the fitted surface for distance to reef, which explained 45% of variation between points. Bottom panels show the fitted surface for tidal amplitude, which explained 62% of variation between points. Left panels show surfaces with sample points for reference, Right panels shows surfaces with species vectors for reference.

Appendix C: Supplementary materials for Chapter 6

Table AC1. The taxon included in each inshore-user functional group in each region.

	Coastal-estuarine fish	Adult reef fish	Juvenile reef fish (marine tolerant)	Juvenile reef fish (brackish tolerant)
Polynesia	Apogonidae spp.	*Acanthurus triostegus*	*Acanthurus blochii*	*Caranx melampygus*
	Mugilidae spp.	*Ctenochaetus striatus*	*Acanthurus triostegus*	*Caranx sexfasciatus*
		Ostorhinchus nigrofasciatus	*Acanthurus xanthopterus*	*Carcharhinus melanopterus*
		Pristiapogon fraenatus	*Ctenochaetus striatus*	*Lutjanus fulvus*
		Balistidae spp.	*Rhinecanthus aculeatus*	*Ellochelon vaigiensis*
		Chaetodon auriga	*Chaetodon auriga*	*Arothron hispidus*
		Chaetodon lunula	*Chaetodon ephippium*	
		Chaetodon lunulatus	*Chaetodon lunula*	
		Chaetodon vagabundus	*Chaetodon vagabundus*	
		Diodon hystrix	*Epibulus insidiator*	
		Neoniphon sammara	*Monotaxis heterodon*	
		Holocentridae spp.	*Lutjanus kasmira*	
		Labridae spp.	*Lutjanus monostigma*	
		Cheilinus chlorourus	*Mulloidichthys flavolineatus*	
		Mulloidichthys flavolineatus	*Parupeneus barberinus*	
		Mulloidichthys vanicolensis	*Upeneus taeniopterus*	
		Ostracion meleagris	*Parupeneus ciliatus*	
		Polydactylus sexfilis	*Ostracion cubicus*	
		Pomacentridae spp.	*Abudefduf sexfasciatus*	
		Abudefduf sexfasciatus	*Abudefduf sordidus*	
		Stegastes nigricans	Scarine spp.	
		Stegastes punctatus	*Chlorurus spilurus*	
		Hipposcarus longiceps	*Scarus altipinnis*	
		Scarus psittacus	*Scarus psittacus*	
		Siganus argenteus		
		Canthigaster valentini		
		Zanclus cornutus		
	Coastal-estuarine fish	**Adult reef fish**	**Juvenile reef fish (marine tolerant)**	**Juvenile reef fish (brackish tolerant)**
New Britain	Ambassidae spp.	*Acanthurus auranticavus*	*Acanthurus* spp.	*Caranx ignobilis*
	Apogonidae spp.	*Fibramia ceramensis*	*Acanthurus auranticavus*	*Caranx papuensis*
	Sphaeramia orbicularis	*Meiacanthus* sp. 1	*Lutjanus biguttatus*	*Caranx sexfasciatus*

	Yarica hyalosoma	*Chaetodon vagabundus*	*Lutjanus boutton*	*Lutjanus argentimaculatus*
	Ophiocara porocephala	*Heniochus acuminatus*	*Lutjanus semicinctus*	*Lutjanus ehrenbergii*
	Gerres filamentosus	Labridae spp.	*Mulloidichthys flavolineatus*	*Lutjanus fulvus*
	Pomadasys argenteus	*Labroides dimidiatus*	*Pentapodus trivittatus*	*Lutjanus russellii*
	Leiognathidae spp.	*Halichoeres* sp. 3	*Scolopsis affinis*	*Scolopsis ciliata*
	Leiognathus equulus	*Lutjanus argentimaculatus*	*Siganus lineatus*	*Pomacentrus tripunctatus*
	Lutjanus goldiei	*Mulloidichthys flavolineatus*		*Siganus fuscescens*
	Lutjanus maxweberi	*Parupeneus indicus*		
	Monodactylus argenteus	*Scolopsis ciliata*		
	Mugilidae spp.	*Abudefduf lorenzi*		
	Upeneus tragula	*Neopomacentrus bankieri*		
	Scatophagus argus	*Pomacentrus tripunctatus*		
	Epinephelus polystigma	*Stegastes nigricans*		
	Mesopristes argenteus	*Siganus fuscescens*		
	Terapon Jarbua	*Siganus lineatus*		
	Chelonodon patoca	Sphyraenidae		
	Toxotes jaculatrix	*Arothron hispidus*		
	Coastal-estuarine fish	**Adult reef fish**	**Juvenile reef fish (marine tolerant)**	**Juvenile reef fish (brackish tolerant)**
North Eastern Australia	Ambassidae spp.	*Acanthurus auranticavus*	*Acanthurus* spp.	Carangidae spp.
	Apogonidae spp.	*Fibramia ceramensis*	Labridae spp.	*Caranx sexfasciatus*
	Yarica hyalosoma	*Meiacanthus* sp. 1	*Lethrinus* spp.	*Carcharhinus melanopterus*
	Scomberoides lysan tol	*Caranx ignobilis*	*Lethrinus obsoletus*	*Plectorhinchus gibbosus*
	Clupeiform spp.	*Caranx papuensis*	*Lutjanus carponotatus*	*Lethrinus harak*
	Gerres filamentosus	*Gnathanodon speciosus*	*Scolopsis lineata*	*Lutjanus argentimaculatus*
	Gerres oyena	*Chaetodon auriga*	*Pomacentrus* spp.	*Lutjanus fulviflamma*
	Pomadasys kaakan	*Chaetodon lineolatus*	Scarine spp.	*Lutjanus russellii*
	Lates calcarifer	*Chaetodon vagabundus*	*Scarus rivulatus*	*Abudefduf bengalensis*
	Leiognathidae spp.	*Labridae* unknown	*Siganus lineatus*	*Pomacentrus tripunctatus*
	Leiognathus equulus	*Choerodon anchorago*		*Epinephelus coioides*
	Nuchequula gerreoides	*Halichoeres miniatus*		*Siganus* spp.
	Monodactylus argenteus	*Lethrinus lentjan*		*Siganus fuscescens*
	Mugilidae spp.	*Lethrinus harak*		*Sphyraene barracuda*
	Pseudomugil signifer	*Lutjanus argentimaculatus*		Sphyraenidae spp.
	Scatophagus argus	*Parupeneus indicus*		
	Selenotoca multifasciata	*Pomacanthus sexstriatus*		
	Sillago analis	*Neopomacentrus bankieri*		
	Sillago ciliata	*Scarus rivulatus*		

	Sillago sihama	Serranidae spp.		
	Acanthropagrus spp.	*Siganus lineatus*		
	Acanthopagrus australis	Sphyraenidae spp.		
	Acanthopagrus pacificus	*Sphyraene barracuda*		
	Mesopristes argenteus			
	Arothron manilensis			
	Chelonodon patoca			
	Toxotes chatareus			
	Coastal-estuarine fish	**Adult reef fish**	**Juvenile reef fish (marine tolerant)**	**Juvenile reef fish (brackish tolerant)**
North Western Australia	Ambassidae spp.			Carangidae spp.
	Ariidae spp.			*Caranx papuensis*
	Clupeiform spp.			*Caranx sexfasciatus*
	Gerres filamentosus			*Plectorhinchus gibbosus*
	Gerres oyena			*Lutjanus argentimaculatus*
	Lates calcarifer			*Lutjanus russellii*
	leiognathidae spp.			
	Photopectoralis bindus			
	Lutjanus johnii			
	Monodactylus argenteus			
	Mugilidae spp.			
	Selenotoca multifasciata			
	Sillago analis			
	Acanthopargus palmaris			
	Amniataba caudavittata			
	Arothron manilensis			

Table AC2. The taxon included in each eco-functional group (based on diet and body-size) in each region.

size	**small**	**small**	**large**	**small**	**large**
diet	**Planktivore**	**Herbivore**	**Herbivore**	**Zoobenthivore - sessile**	**Zoobenthivore - sessile**
Polynesia	Apogonidae	*Acanthurus blochii* JP	*Acanthurus triostegus*	*Chaetodon auriga* JP	*Chaetodon auriga*
	Ellochelon vaigiensis JP	*Acanthurus triostegus* JP	*Ctenochaetus striatus* Adult	*Chaetodon lunulatus*	*parupeneus barberinus* JP
		Acanthurus xanthopterus JP	Mugilidae		*Zanclus cornutus*
		Ctenochaetus striatus JP	*Hipposcarus longiceps*		
		Mugilid JP	*Scarus psittacus* Adult		
		Stegastes nigricans	*Siganus argenteus*		
		Stegastes punctatus			
		Scarine spp. EJP			
		Chlorurus spilurus EJP			
		Scarus spp. LJP			
		Scarus altipinnis EJP			
		Scarus psittacus LJP			
		Scarus psittacus EJP			
size	**small**	**small**	**large**	**small**	**large**
diet	**Planktivore**	**Herbivore**	**Herbivore**	**Zoobenthivore - sessile**	**Zoobenthivore - sessile**
New	Apogonidae	*Pomacentrus tripunctatus* JP	Mugilidae	*Parupeneus indicus* Adult	
Britain	*Sphaeramia orbicularis*	*Pomacentrus tripunctatus* Adult	*Siganus fuscescens* Adult		
	Neopomacentrus bankieri	*Siganus fuscescens* LJP	*Siganus lineatus* Adult		
		Siganus lineatus JP			
		Chelonodon patoca JP			
size	**small**	**small**	**large**	**small**	**large**
diet	**Planktivore**	**Herbivore**	**Herbivore**	**Zoobenthivore - sessile**	**Zoobenthivore - sessile**
North	Apogonidae	*Pomacentrus tripunctatus* JP	*Acanthurus auranticavus*	*Parupeneus indicus* Adult	*Gnathanodon speciosus*
Eastern	Clupeiform	*Pomacentrus* spp. JP	*Mugilidae*		*Chaetodon auriga*
Australia	*Neopomacentrus bankieri*	*Siganus* spp. EJP	*Scarus rivulatus* JP		*Chaetodon lineolatus*
		Siganus fuscescens EJP	*Scarus rivulatus* Adult		Dasyatidae
		Siganus lineatus JP	*Siganus lineatus* Adult		*Chelonodon patoca*
size	**small**	**small**	**large**	**small**	**large**
diet	**Planktivore**	**Herbivore**	**Herbivore**	**Zoobenthivore - sessile**	**Zoobenthivore - sessile**
North Western Australia			Mugilidae		

size	small	large	small	large	large
diet	**Omnivore**	**Omnivore**	**Zoobethivore - mobile**	**Zoobethivore - mobile**	**Piscivore**
Polynesia	*Chaetodon ephippium* JP *Chaetodon vagabundus* JP *Ostracion meleagris* *Ostracion cubicus* JP *Abudefduf sexfasciatus* JP *Abudefduf sordidus* JP *Stegastes nigricans* *canthigaster valentini*	*Chaetodon vagabundus* *Abudefduf sexfasciatus* *Arothron hispidus* JP	*Ostorhinchus nigrofasciatus* *Pristiapogon fraenatus* *Rhinecanthus aculeatus* JP *Chaetodon lunula* JP Gobiform *Epibulus insidiator* EJP *Monotaxis heterodon* JP *Lutjanus fulvus* EJP *Mulloidichthys flavolineatus* JP *Upeneus taeniopterus* JP *Parupeneus ciliatus* EJP	*Chaetodon lunula* *Diodon hystrix* *Cheilinus chlorourus* *Mulloidichthys flavolineatus* Adult *Mulloidichthys vanicolensis* Adult *Mulloidichthys vanicolensis* JP	*Caranx melampygus* JP *Carcharhinus melanopterus* JP *Neoniphon sammara* Holocentridae *Lutjanus fulvus* LJP *Lutjanus monostigma* JP *Polydactylus sexfilis*

size	small	large	small	large	large
diet	**Omnivore**	**Omnivore**	**Zoobethivore - mobile**	**Zoobethivore - mobile**	**Piscivore**
New Britain	*Monodactylus argenteus* JP *Stegastes nigricans* *Mesopristes argenteus* JP	*Chaetodon vagabundus* *Monodactylus argenteus* *Abudefduf lorenzi* *Scatophagus argus* *Mesopristes argenteus* Adult *Terapon Jarbua* Adult *Arothron hispidus* *Toxotes jaculatrix*	Ambassidae *Fibramia ceramensis* *Yarica hyalosoma* *Meiacanthus* sp. 1 Gobiform *Labroides dimidiatus* *Lutjanus argentimaculatus* EJP *Lutjanus biguttatus* EJP *Lutjanus boutton* JP *Lutjanus ehrenbergii* JP *Lutjanus fulviflamma* LJP *Lutjanus fulvus* EJP *Lutjanus maxweberi* JP *Lutjanus maxweberi* Adult *Lutjanus russellii* EJP *Mulloidichthys flavolineatus* JP *Upeneus tragula* JP *Pentapodus trivittatus* EJP *Scolopsis affinis* EJP *Scolopsis ciliata* EJP	*Ophiocara porocephala* *Gerres filamentosus* *Pomadasys argenteus* *Leiognathidae* *Leiognathus equulus* *Lutjanus argentimaculatus* LJP *Lutjanus russellii* LJP *Mulloidichthys flavolineatus* *Scolopsis ciliata* Adult	*Caranx ignobilis* JP *Caranx papuensis* JP *Caranx sexfasciatus* LJP *Lutjanus argentimaculatus* Adult *Lutjanus fulvus* LJP *Lutjanus goldiei* Adult *Epinephelus polystigma* EJP *Epinephelus polystigma* Adult

size	small	large	small	large	large
diet	**Omnivore**	**Omnivore**	**Zoobethivore - mobile**	**Zoobethivore - mobile**	**Piscivore**
North Eastern Australia	*Abudefduf bengalensis* JP	*Chaetodon vagabundus* *Monodactylus argenteus* *Pomacanthus sexstriatus* *Scatophagus argus* *Selenotoca multifasciata* *Mesopristes argenteus* Adult *Arothron manilensis* *Toxotes chatareus*	Ambassidae Fibramia ceramensis yarica hyalosoma meiacanthus sp. 1 Gobiform *Halichoeres miniatus* Labridae spp. JP *Nuchequula gerreoides* *Lethrinus* spp. EJP *Lutjanus fulviflamma* EJP *Lutjanus fulviflamma* LJP *Lutjanus russellii* EJP *Scolopsis lineata* EJP *Pseudomugil signifer* *Acanthopagrus* JP	*Gerres filamentosus* *Gerres oyena* *Pomadasys kaakan* *Plectorhinchus gibbosus* JP *Choerodon anchorago* Adult Leiognathidae *Leiognathus equulus* *Lethrinus lentjan* Adult *Lutjanus argentimaculatus* LJP *Lutjanus carponotatus* LJP *Lutjanus russellii* LJP *Sillago analis* Adult *Sillago ciliata* *Sillago sihama* *Acanthopagrus australis* *Acanthopagrus pacificus* *Acanthopargus palmaris*	Carangidae spp. JP *Caranx ignobilis* Adult *Caranx papuensis* Adult *Caranx sexfasciatus* LJP *Scomberoides spp.* *Scomberoides lysan* *Carcharhinus melanopterus* JP *Lates calcarifer* *Lethrinus harak* LJP *Lethrinus harak* Adult *Lutjanus argentimaculatus* Adult *Epinephelus coioides* JP *Sphyraene barracuda* *Sphyraene barracuda* JP
size	**small**	**large**	**small**	**large**	**large**
diet	**Omnivore**	**Omnivore**	**Zoobethivore - mobile**	**Zoobethivore - mobile**	**Piscivore**
North Western Australia		*Amniataba caudavittata*	Ambassidae *Caranx sexfasciatus* EJP Gobiform *Photopectoralis bindus* *Lutjanus johnii* EJP *Sillago analis* JP	*Drepane punctata* *Gerres filamentosus* Leiognathidae *Lutjanus argentimaculatus* LJP *Acanthopargus palmaris* *Acanthopagrus spp. Adult*	*Lates calcarifer* *Lutjanus johnii* Adult *Sphyraene barracuda*

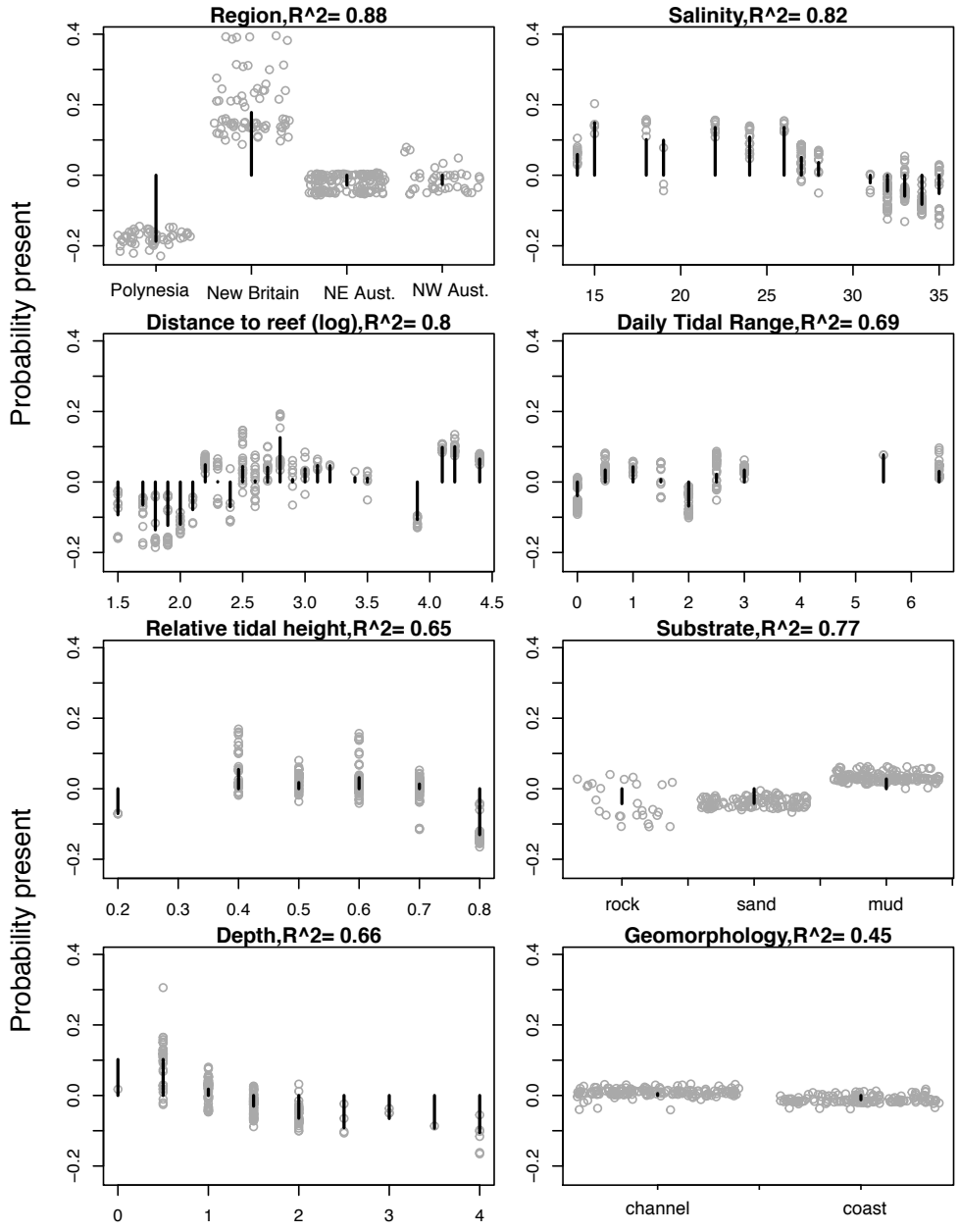


Figure AC1. The ranked contribution of all variables to a Random Forest predication model of coastal-estuarine fish presence in mangrove habitat. Variable plots are displayed in ranked order of importance from left to right. Grey circles show the influence of the contextual variable on class prediction for each observation, black bars show average values, indicating the magnitude of positive or negative contribution. Goodness of fit of each variable is displayed (R^2).

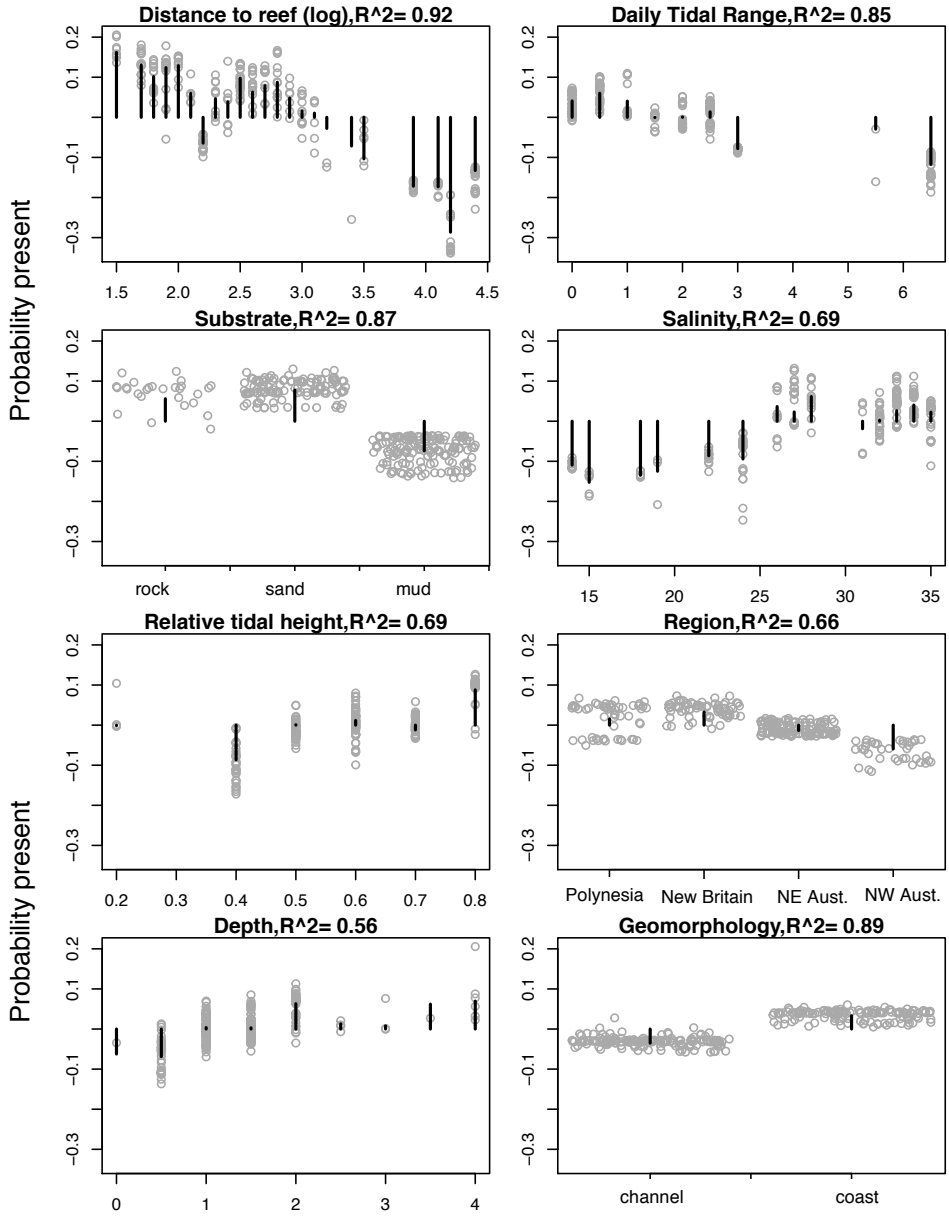


Figure AC2. The ranked contribution of all variables to a Random Forest predication model of adult reef fish presence in mangrove habitat. Variable plots are displayed in ranked order of importance from left to right. Grey circles show the influence of the contextual variable on class prediction for each observation, black bars show average values, indicating the magnitude of positive or negative contribution. Goodness of fit of each variable is displayed (R^2).

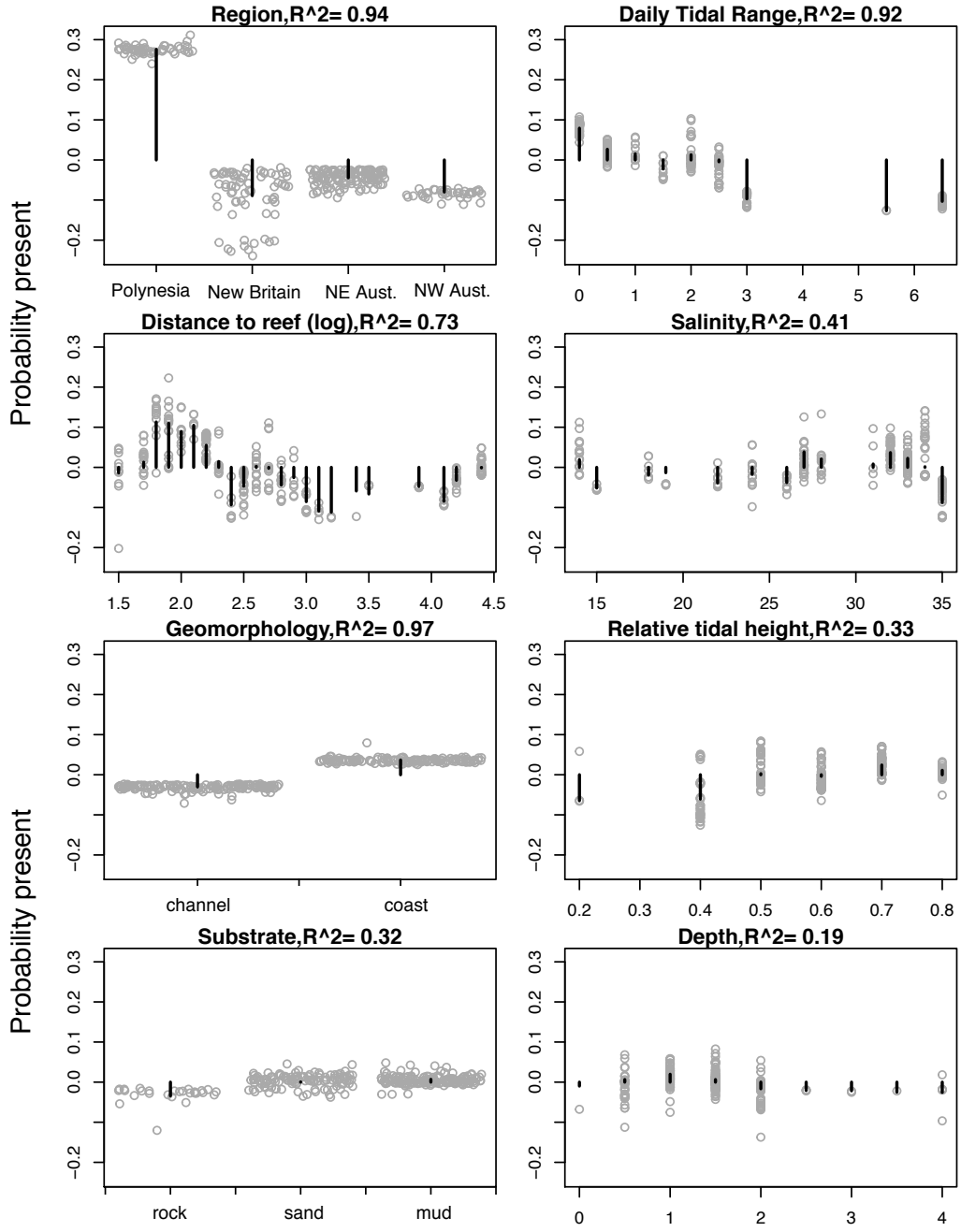


Figure AC3. The ranked contribution of all variables to a Random Forest predication model of juvenile marine reef fish presence in mangrove habitat. Variable plots are displayed in ranked order of importance from left to right. Grey circles show the influence of the contextual variable on class prediction for each observation, black bars show average values, indicating the magnitude of positive or negative contribution. Goodness of fit of each variable is displayed (R^2).

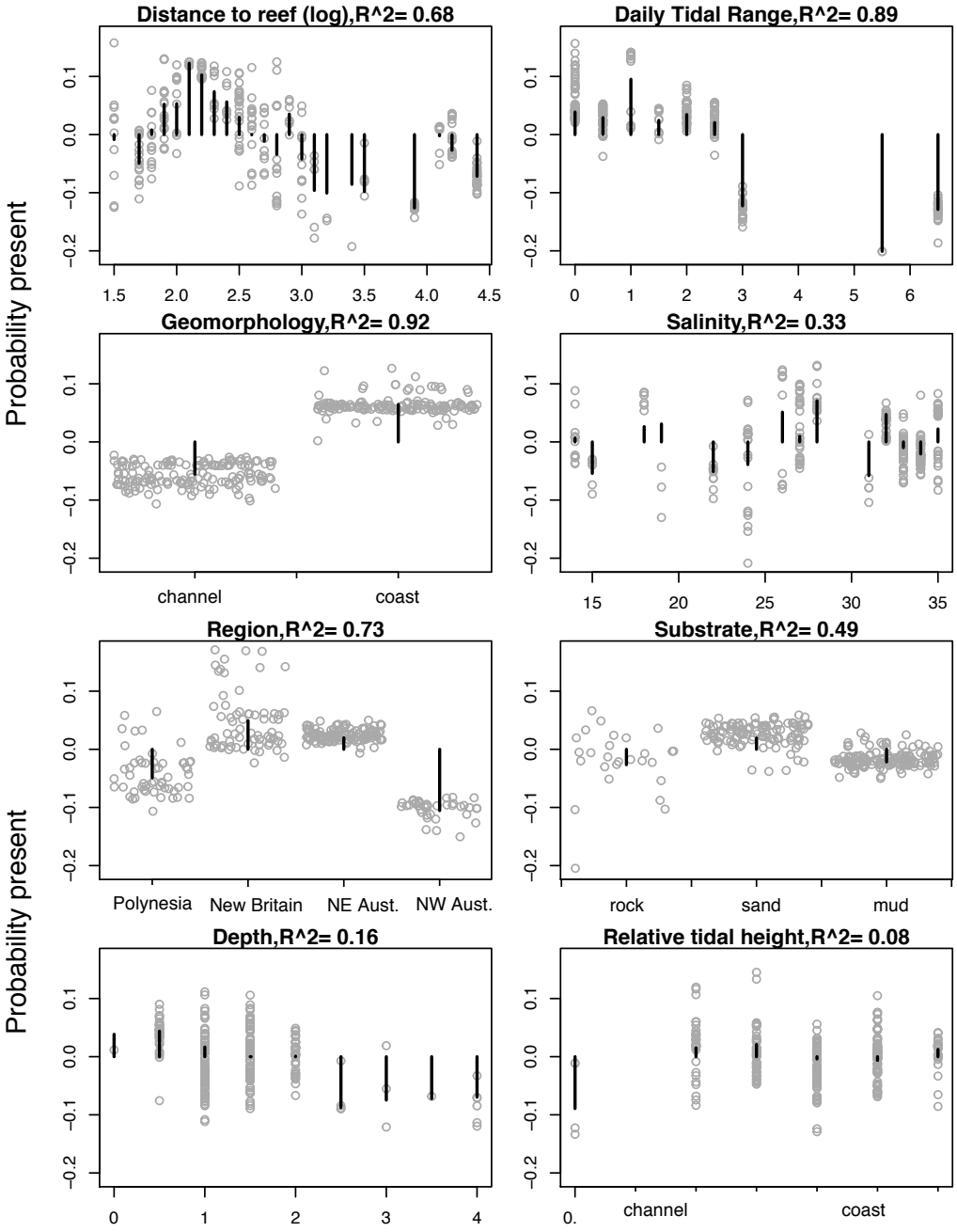


Figure AC4. The ranked contribution of all variables to a Random Forest predication model of juvenile brackish-tolerant reef fish presence in mangrove habitat. Variable plots are displayed in ranked order of importance from left to right. Grey circles show the influence of the contextual variable on class prediction for each observation, black bars show average values, indicating the magnitude of positive or negative contribution. Goodness of fit of each variable is displayed (R^2).

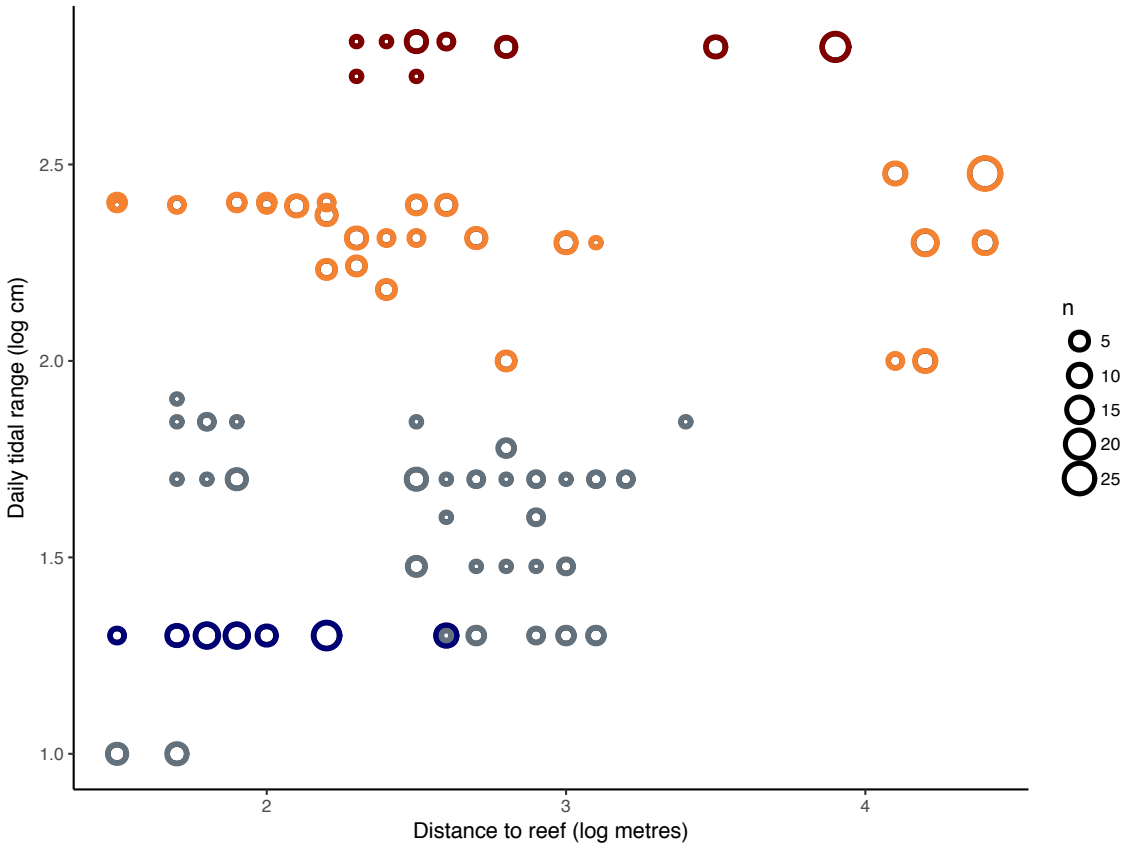


Figure AC5. Distribution of sampled range shown for daily tidal range and distance to reef, by region. Size of circles is proportional to the number of samples at that point in contextual space, and the colour of circles corresponds to region: dark-blue for Polynesia, grey for New Britain, orange for North Eastern Australia, and red for North western Australia.

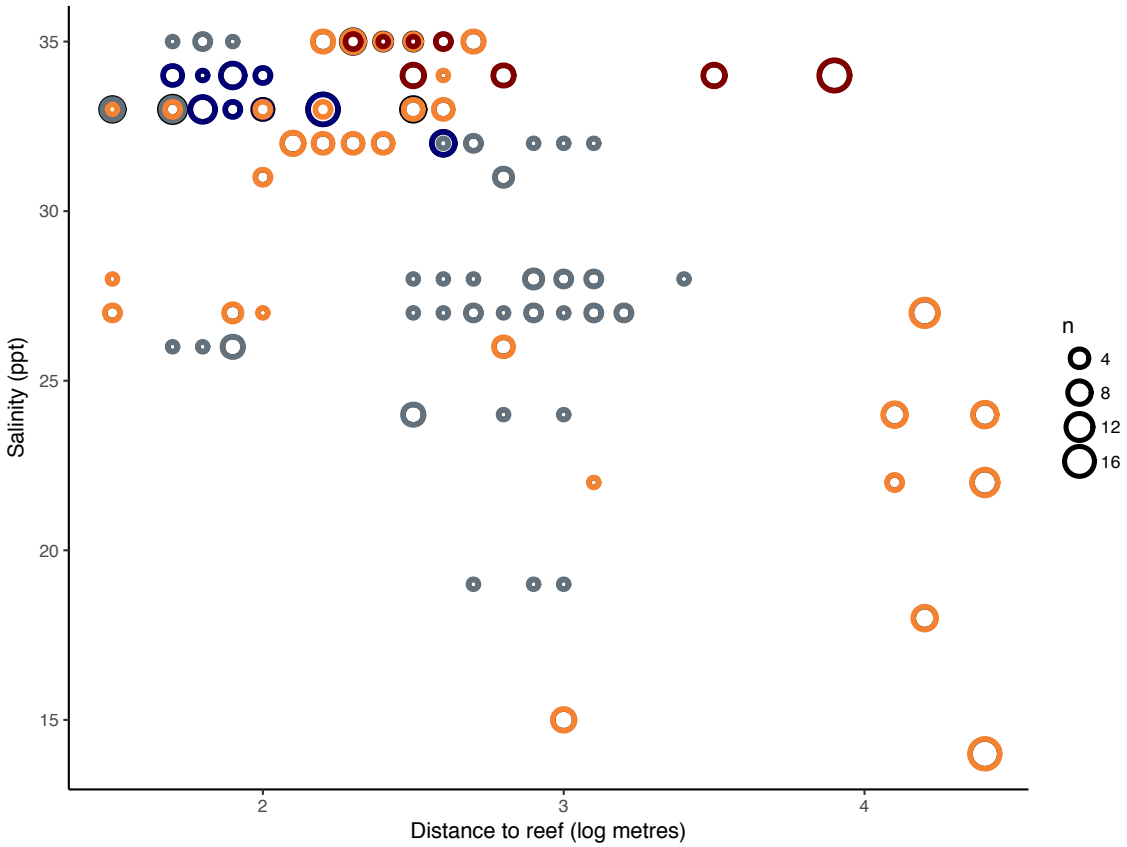
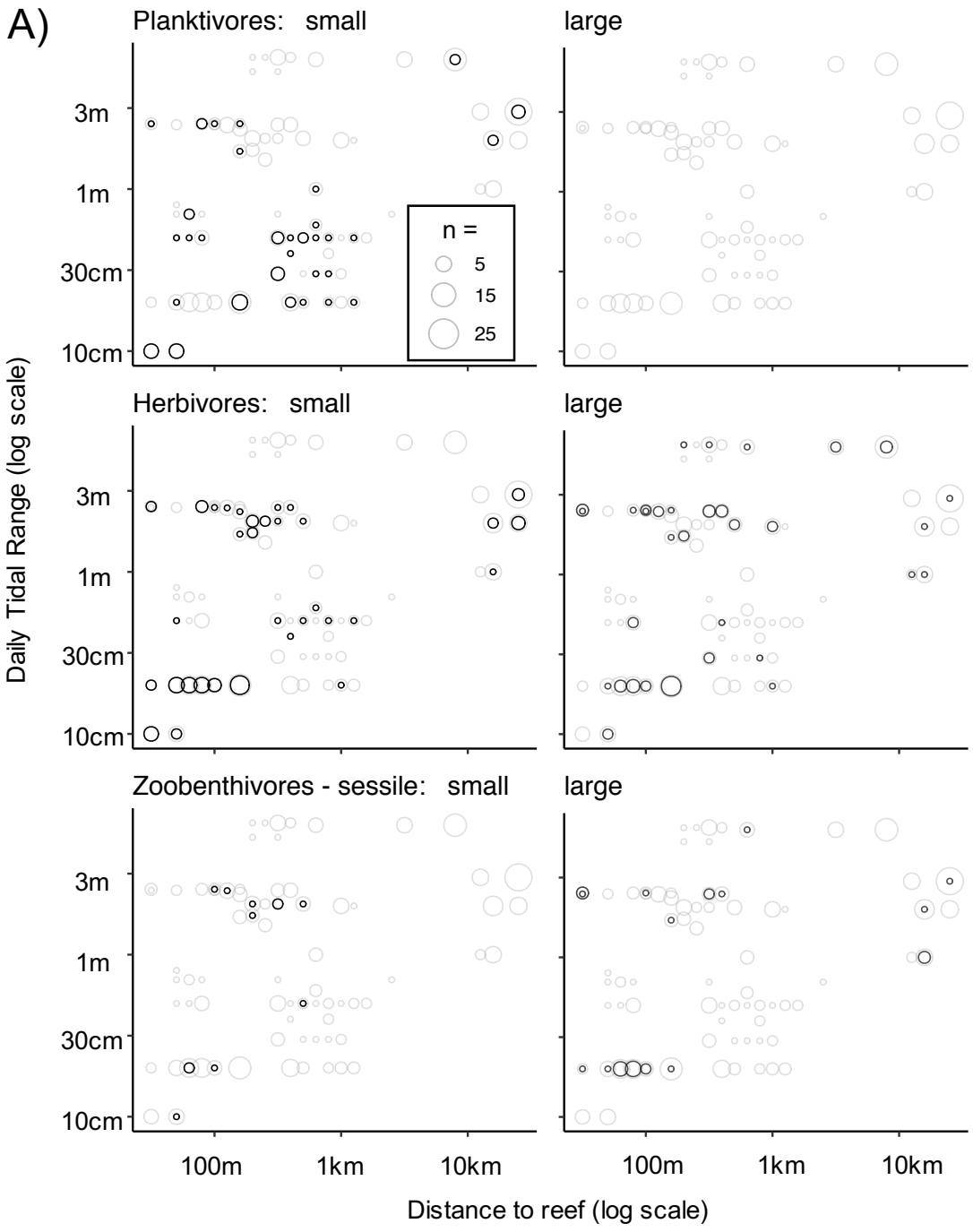


Figure AC6. Distribution of sampled range shown for salinity and distance to reef, by region. Size of circles is proportional to the number of samples at that point in contextual space, and the colour of circles corresponds to region: dark-blue for Polynesia, grey for New Britain, orange for North Eastern Australia, and red for North western Australia.

Appendix text AC1:

Distribution of eco-functional groups

There were clear patterns in the distribution of eco-functional (diet and body-size) groups relative to environmental context. The use of mangroves by individual eco-functional groups was examined according to the contextual variables that were important in defining assemblage composition in community analysis (Figure 6.9) – tidal range, distance to reef, and salinity. The distribution of body size varied considerably. In general, small bodied fish were absent from mangroves in large tidal amplitude contexts, while large bodied fish were found throughout contextual space (Figure AC7). Small bodied omnivores, herbivores, planktivores, and zoobenthivores that prey on sessile invertebrates, all tended to be absent from large tidal range contexts. For omnivores, and zoobenthivores that prey on sessile invertebrates, small bodied individuals were restricted to contexts with moderate tidal ranges that are also close to reefs. The groups were present close to reefs in the full range of salinities in these locations (35-25ppt, Figure AC8). The notable exception to these patterns was that small zoobenthivores that prey on mobile invertebrates were consistently present in mangroves – including in large tidal range contexts.


A)
Planktivores: small
large
Herbivores: small
large
Zoobenthivores - sessile: small
large
3m
1m
30cm
10cm
n =
5
15
25
Daily Tidal Range (log scale)
100m
1km
10km
Distance to reef (log scale)

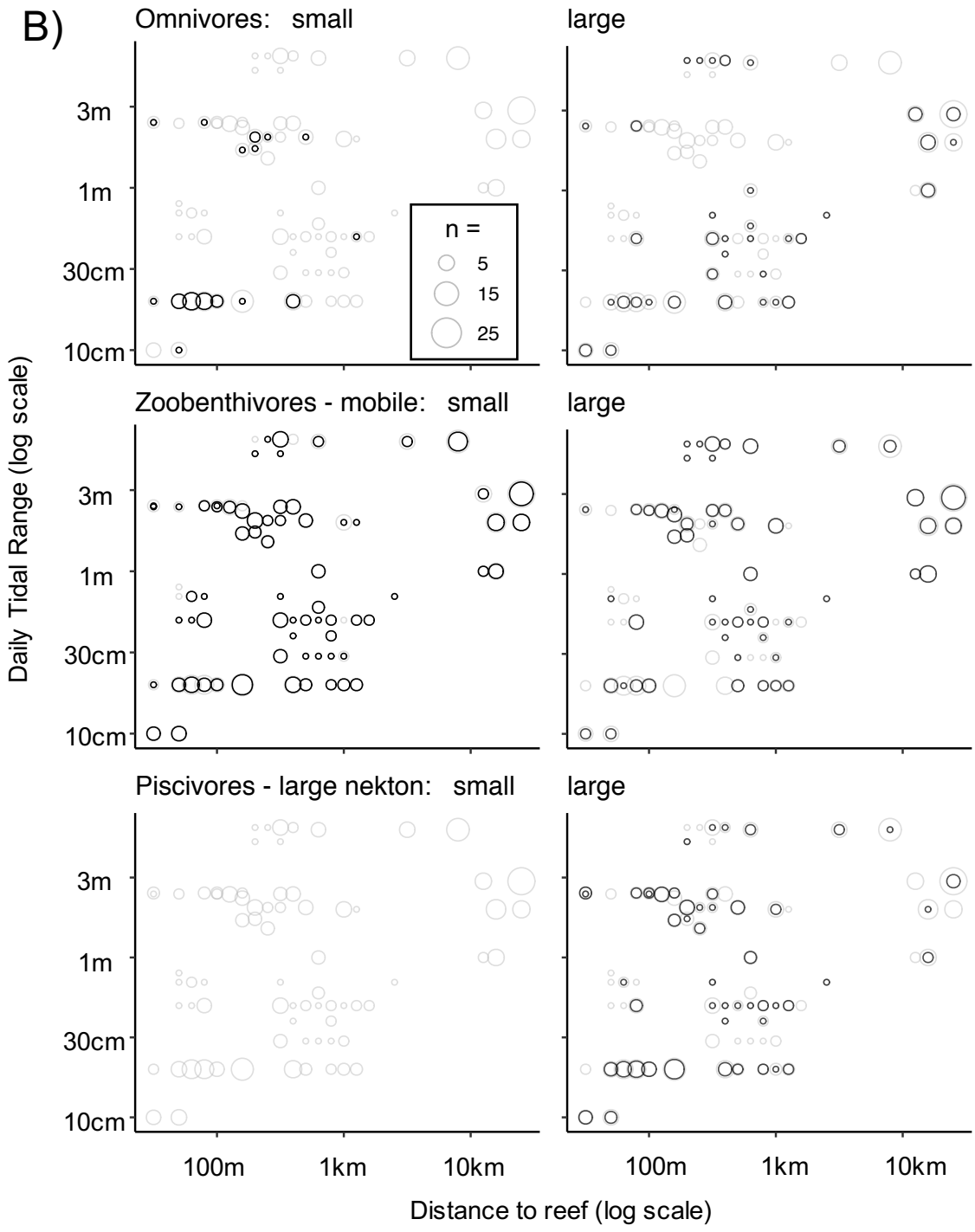
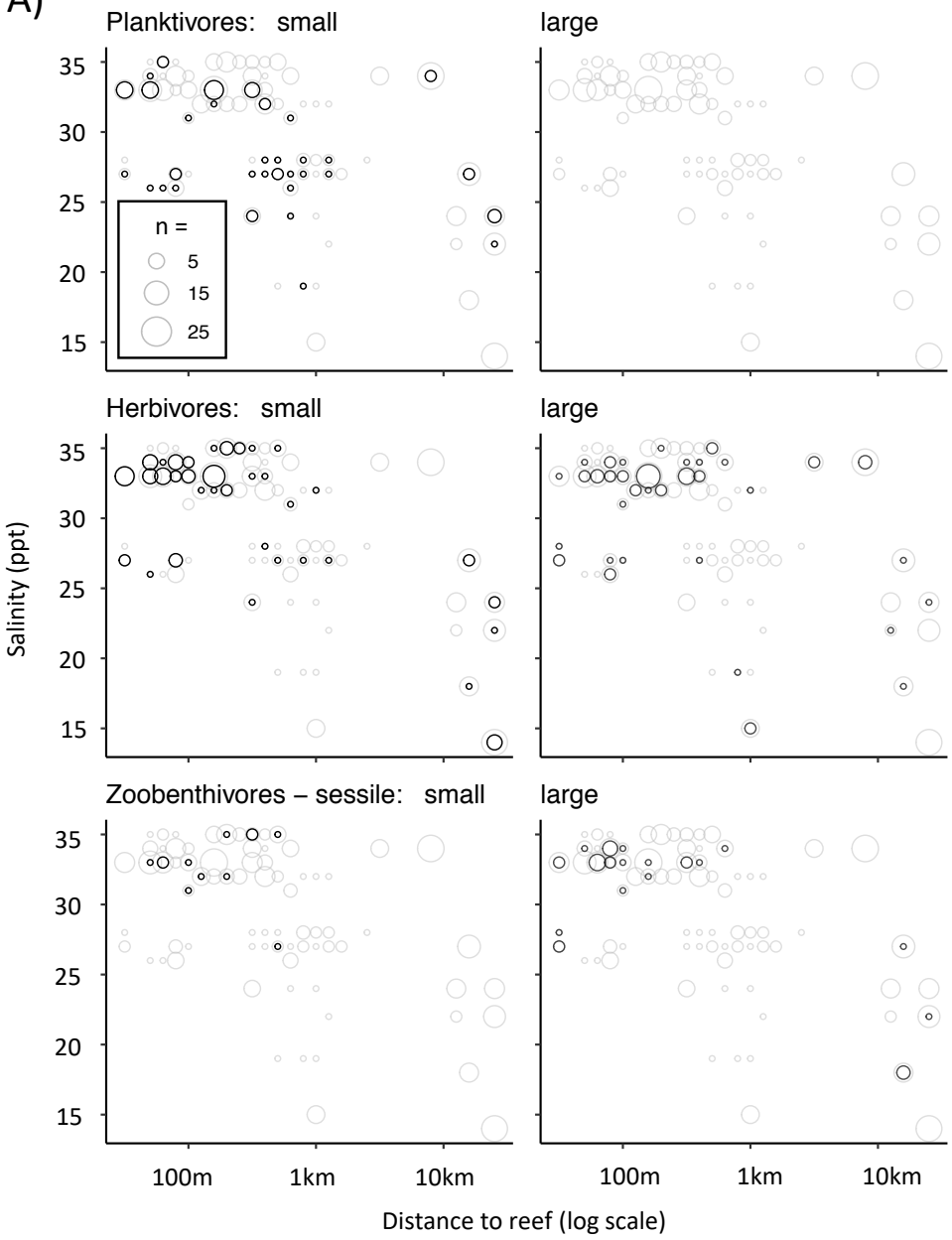


Figure AC7 A&B. Distribution of eco-functional groups according to tidal range and distance to reef. Size of circles is proportional to the number of samples at that point in contextual space. Black circles represent eco-functional group occurrence, and grey circles show the total sampling effort (n = 297).

A)


Planktivores: small
large
Herbivores: small
large
Zoobenthivores – sessile: small
large
n =
5
15
25
Salinity (ppt)
35
30
25
20
15
100m
1km
10km
Distance to reef (log scale)

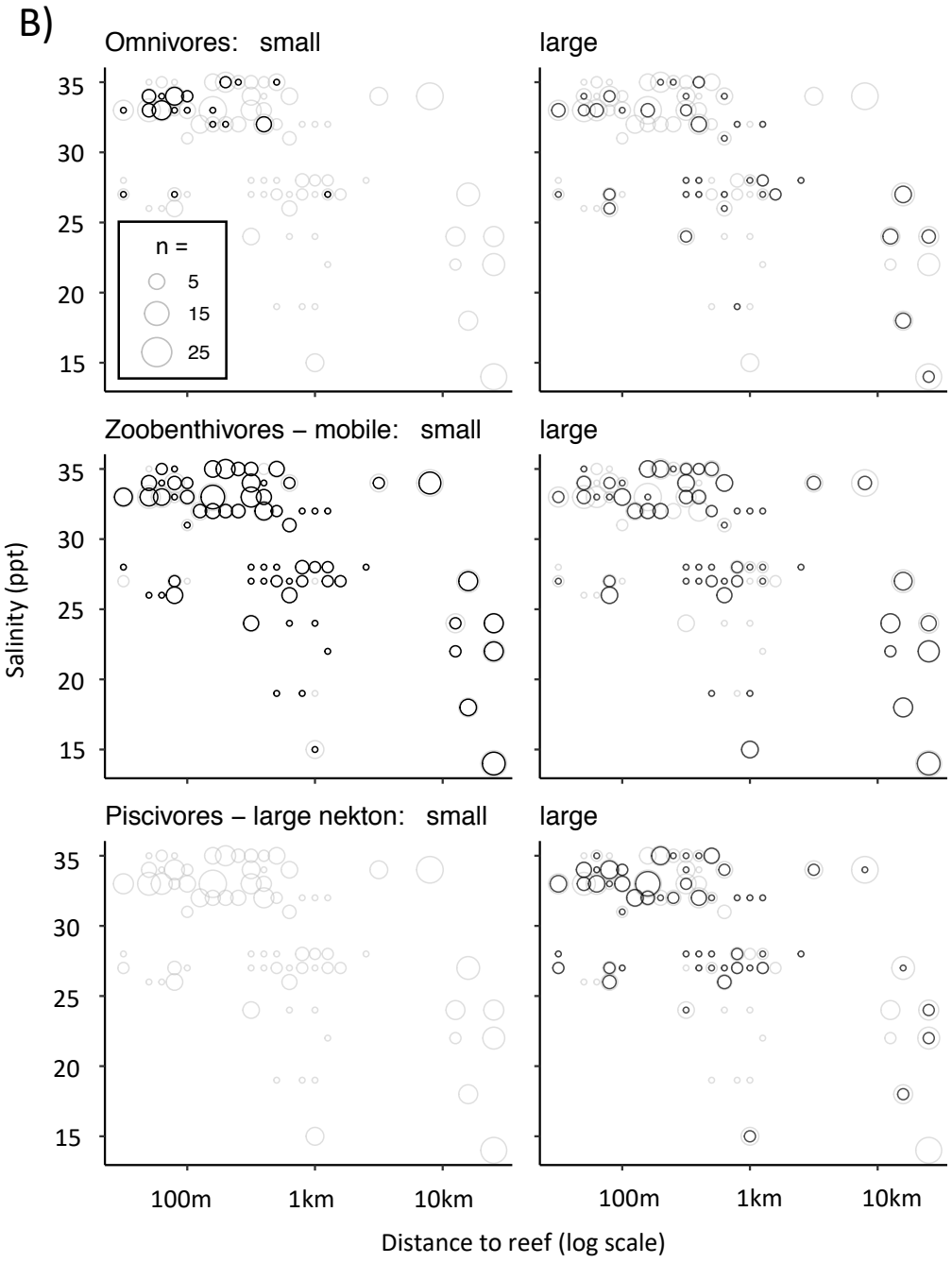


Figure AC8 A&B. Distribution of eco-functional groups according to salinity and distance to reef. Size of circles is proportional to the number of samples at that point in contextual space. Black circles represent eco-functional group occurrence, and grey circles show the total sampling effort (n = 297).

Appendix D: Contrasting Seascape Use by a Coastal Fish Assemblage: a Multi-methods Approach.

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Contrasting Seascape Use by a Coastal Fish Assemblage: a Multi-methods Approach

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Abstract

Understanding the range of habitats needed to complete life-cycles is essential for the effective conservation and management of species. We combined otolith microchemistry, acoustic tracking, and underwater video to determine patterns of seascape use by an assemblage of tropical snappers, including two little-known species of high economic importance, the Papuan black bass (*Lutjanus goldiei*) and spot-tail snapper (*Lutjanus fuscescens*). All species appeared to have marine larval phases, and post-settlement distributions broadly overlapped across the coastal seascape. However, species and life stages were distributed along a gradient from freshwater to coastal waters. *Lutjanus fuscescens* is primarily a freshwater species post-settlement, but larger individuals move into brackish estuaries and even coastal waters at times. *Lutjanus goldiei* appear to recruit to low salinity or freshwater areas. Larger individuals tend to have home-ranges centred on brackish estuaries, while making regular movements into both coastal waters and freshwater. *Lutjanus argentimaculatus* also ranged widely from fresh to coastal waters, but juveniles were most common in the saline parts of estuaries. Ontogenetic shifts by *L. argentimaculatus* were similar to those reported from other regions, despite vast differences in the spatial proximity of seascape components. The wide-ranging seascape movements of our target species highlight the importance of maintaining effective connectivity between marine, estuarine, and freshwaters in the region to maintain ecosystem function and support sustainable sport fisheries. The combined approaches resolved some of the ambiguities of individual methods and provide a powerful approach to understanding seascape use by coastal fishes.

Keywords Ontogeny · Connectivity · Otolith microchemistry · Acoustic tracking · Underwater video

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